

A new apheliscine “condylarth” mammal from the late Paleocene of Montana and Alberta and the phylogeny of “hyopsodontids”

SHAWN P. ZACK, TONYA A. PENKROT, DAVID W. KRAUSE, and MARY C. MAAS



Zack, S.P., Penkrot, T.A., Krause, D.W., and Maas, M.C. 2005. A new apheliscine “condylarth” mammal from the late Paleocene of Montana and Alberta and the phylogeny of “hyopsodontids”. *Acta Palaeontologica Polonica* 50 (4): 809–830.

We describe a new genus, including at least two species, of apheliscine “condylarth,” *Gingerichia geoteretes* from Douglass and Glennie quarries in the eastern Crazy Mountains Basin, south-central Montana, and *Gingerichia hystrix* from Cochrane 2, in Alberta, Canada, both late Paleocene (early Tiffanian; Ti1) sites. *Gingerichia geoteretes* is based on a nearly complete lower cheek dentition and is distinctive among apheliscines in lacking paraconid, metaconid, and anterior cingulid on p4 and possessing lower molars with less reduced paraconids (particularly m2 and m3) and relatively elevated trigonids. *Gingerichia hystrix* appears to represent a slightly older species and its morphology is slightly less specialized than that of *G. geoteretes*. These taxa are rare elements in the Cochrane 2 and Douglass Quarry assemblages and are the earliest known apheliscines; they therefore provide a new opportunity to elucidate both the composition and the phylogenetic relationships of the Apheliscinae and other small-bodied “condylarths.” Phylogenetic analysis indicates that *Hyopsodus* and mioclaenids form a monophyletic group that excludes other taxa traditionally placed in Hyopsodontidae, including apheliscines. Accordingly, Hyopsodontidae is redefined to include the traditional contents of Mioclaenidae. Other “hyopsodontids,” including apheliscines, form a monophyletic clade, and Apheliscidae is revived to accommodate this group. Finally, we recognize *Haplaletes serior* as the lower dentition of *Utemylus latomius* or a close relative.

Key words: Mammalia, “Condylarthra,” Apheliscidae, Hyopsodontidae, Paleocene, Tiffanian, N. America.

Shawn P. Zack [szack1@jhmi.edu] and Tonya A. Penkrot [tpenkrot@jhmi.edu], Center for Functional Anatomy & Evolution, The Johns Hopkins University School of Medicine, Baltimore, Maryland 21205;

David W. Krause [dkrause@notes.cc.sunysb.edu], Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794-8081;

Mary C. Maas [mcmaas@prodigy.net.mx], Department of Anthropology and Laboratory of Vertebrate Paleontology, University of Texas at Austin, Austin, Texas 78712-1086.

Introduction

Classification of small-bodied, dentally bunodont early Tertiary mammals has been a persistent problem in mammalian paleontology. The vast majority of these species, though important components of their faunas, are known almost exclusively from dental remains. Several distantly related clades, including “hyopsodontid” and mioclaenid “condylarths,” erinaceomorph lipotyphlans, and pentacodontid pantolestans have proven difficult to distinguish because of convergent similarities in dental morphology (Rigby 1980; Bown and Schankler 1982; Gingerich 1983; Novacek et al. 1985) and the scarcity of potentially more diagnostic cranial fossils. The Paleocene–Eocene Apheliscinae provides a good illustration of the difficulties in assessing the higher-level affinities of such small, bunodont taxa. Apheliscinae minimally includes two relatively well-known genera, *Apheliscus* Cope, 1875 and *Phenacodaptes* Jepsen, 1930, from the late Paleocene and early Eocene of North America (Gazin 1959; Rose 1981;

Gingerich 1994). *Apheliscus* and *Phenacodaptes* share numerous synapomorphies in molar and, particularly, premolar morphology (enlarged P4 and p4 dominated by paracone and protoconid; steep prevallum and postvallid on P4 and p4; simplified, unbasined p4 talonid). Since Gazin (1959) first presented evidence of a close relationship, monophyly of *Apheliscus* and *Phenacodaptes* has been widely accepted (Van Valen 1967, 1978; Rose 1981; McKenna and Bell 1997; Archibald 1998). The broader relationships of the clade, however, have been much more contentious.

Gazin (1959) proposed that apheliscines are closely related to pentacodontid pantolestans, citing striking similarities in premolar morphology in support of this hypothesis. While this conclusion was accepted by Rigby (1980), most subsequent workers have viewed the premolar similarities to pentacodontids as convergent and have favored affinities to the paraphyletic basal ungulate order “Condylarthra” for apheliscines based on similarities in molar morphology. In particular, most authors have endorsed McKenna’s (1960)

argument that apfeliscines are “condylarths” related to either “Hyopsodontidae” or Mioclaenidae (Van Valen 1967, 1978; Delson 1971; Rose 1981; Gingerich 1994; McKenna and Bell 1997; Archibald 1998). No worker has postulated a close relationship to Erinaceomorpha, although Bown and Schankler (1982) proposed a relationship to *Adapisorex*, which they considered to be a “condylarth” but which is generally placed in Erinaceomorpha (Russell 1964; Novacek 1985; Novacek et al. 1985; McKenna and Bell 1997).

Furthermore, there are serious questions about the composition of the clades to which apfeliscines may be related, which complicates attempts to establish their affinities. Mioclaenidae is the least contentious of these groups. Since Simpson’s (1937a) revision of small-bodied Paleocene “condylarths,” the composition of the family has remained relatively stable, aside from the addition of several South American genera described in the past few decades (Muizon and Marshall 1987a, b, 1991; Bonaparte et al. 1993; Muizon and Cifelli 2000). In fact, much of the discussion about this group has centered on whether it deserved familial separation from “Hyopsodontidae.” Most recent workers favor familial status for Mioclaenidae (McKenna and Bell 1997; Archibald 1998; Muizon and Cifelli 2000), largely because of lingering questions about the closeness of the relationship between “hyopsodontids” and mioclaenids.

The composition and diagnosis of “Hyopsodontidae” has been more controversial. Even with the removal of mioclaenids, it has proven difficult to identify derived characters that unite “hyopsodontids” (Cifelli 1983; Archibald 1998). Simpson (1937a) provided a substantial list of diagnostic characters, but many of these are now considered plesiomorphic for “condylarths” and ungulates in general. Complicating attempts to delimit and diagnose “Hyopsodontidae” is the fact that no recent cladistic study has explicitly addressed the composition and interrelationships of “hyopsodontids.” In the few studies that have included some “hyopsodontids” (Rigby 1980; Tabuce et al. 2001; Hooker and Dashzeveg 2003), the phylogeny of the group was tangential to larger goals.

Pentacodontidae was originally named for two genera, *Pentacodon* and *Aphronorus*, which are almost certainly closely related (Simpson 1937a; Gazin 1959; Van Valen 1967). Subsequent workers (Gazin 1956; Van Valen 1967; McKenna and Bell 1997) have expanded the morphologic and taxonomic diversity of pentacodontids, but no author since Simpson (1937a) has revised the diagnosis of the group. Pentacodontids, long contained within the wastebasket taxon ‘Proteutheria,’ most recently have been placed in the diverse order Cimolesta (McKenna and Bell 1997), along with a great many other problematic extinct groups. Cimolesta is itself somewhat poorly defined and may also prove polyphyletic.

We report here on a new genus of small-bodied, bunodont eutherian from several early Tiffanian quarries in Montana and Alberta that shows derived similarities to *Apheliscus* and *Phenacodaptes* and represents the earliest known representa-

tive of Apheliscinae. The new genus shares premolar and molar synapomorphies with previously known apfeliscines mixed with plesiomorphic features—as well as with its own specializations—that help clarify the affinities of *Phenacodaptes* and *Apheliscus*. The identification of the new genus provides an opportunity to revisit the question of apfeliscine relationships and provides further support for a relationship to “hyopsodontids.” As a result, we take the opportunity to present a new phylogenetic analysis designed to test the monophyly of “Hyopsodontidae” and provide a preliminary investigation of “hyopsodontid” interrelationships.

Terminology, measurements, and abbreviations

The phylogenetic analysis presented below substantially changes the composition of the “condylarth” family Hyopsodontidae. Throughout the body of this work, “Hyopsodontidae” and “hyopsodontid” placed in quotation marks refer to the traditional composition of the family, essentially as given in McKenna and Bell (1997). Hyopsodontidae and hyopsodontid when given without quotation marks, unless explicitly stated otherwise, refer to the new composition presented in this work.

All measurements were taken through a Nikon dissecting microscope with a reticle in the eyepiece. Maximum antero-posterior lengths and buccolingual widths were measured to the nearest 0.05 mm. For upper cheek teeth, maximum antero-posterior length was measured from the parastyle to the posteriormost margin of the tooth, and maximum buccolingual width was measured from the buccal cingulum to the lingual extreme of each tooth. For lower cheek teeth, maximum antero-posterior length was measured from the anterior cingulid to the posterior extent of each tooth, and both maximum trigonid and maximum talonid buccolingual widths were measured.

*Institutional abbreviations*¹.—AMNH, American Museum of Natural History, New York; BUNM, Bureau of Land Management Collection, University of New Mexico, Albuquerque, New Mexico; IRScNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; KU, University of Kansas Natural History Museum, Lawrence, Kansas; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN, Muséum national d’Histoire naturelle, Paris, France; SMM, Science Museum of Minnesota, St. Paul, Minnesota; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada; UCMP, University of California, Museum of Paleontology, Berkeley, California; UM, Museum of Paleontology, University of Michigan, Ann Arbor, Michigan; UNM, University of New Mexico, Albuquerque, New Mexico; USGS, United States Geological Survey, Denver registry,

¹ The institutions for which the countries are not provided are in USA.

Denver, Colorado; USNM, United States National Museum of Natural History, Washington D.C.; UW, University of Wyoming Geological Museum, University of Wyoming, Laramie, Wyoming; Wa and WB, Geologisch-Paläontologisches Institut, Halle, Germany; YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut; YPM:PU, Princeton University Collection, Yale Peabody Museum, Yale University, New Haven, Connecticut.

Systematic paleontology

Order “Condylarthra” Cope, 1881

Family Apheliscidae Matthew, 1918

Included taxa.—Apheliscinae Matthew, 1918, Louisininae Sudre and Russell, 1982, *Haplomyilus* Matthew, 1915, *Litomylus* Simpson, 1935, *Haplaletes* Simpson, 1935, *Aletodon* Gingerich, 1977, *Dorraletes* Gingerich, 1983, *Utemylus* Gingerich, 1983.

Revised diagnosis.—Apheliscids can be distinguished from similar taxa including hyopsodontids, pentacodontids, and basal erinaceomorphs by the following combination of features: molars bunodont (in particular, the postmetacrista is nonsalient or only weakly salient); m2 larger than m1; lower molar trigonids somewhat taller than talonids or subequal in height; lower molar paraconids low, well separated from metaconids; lower molar hypoconulid not basally fused to entoconid, not connected to entoconid by a crest, and median in position; and M1–2 hypocone well developed and arising from same level on protocone as anterior cingulum.

Apheliscids for which the tarsus is known can be further distinguished from hyopsodontids by the following features: trochlear groove on astragalus well developed; astragalar foramen absent; trochlear articular surface extends onto posterior surface of astragalus; prominent cotylar fossa present; posteromedial projection of astragalar body absent.

Discussion.—Because the phylogenetic analysis presented below agrees with other cladistically based studies in disassociating *Hyopsodus* from Hyopsodontidae *sensu stricto* (Rigby 1980; Tabuce et al. 2001; Hooker and Dashzeveg 2003), we feel it is appropriate to separate *Hyopsodus* from other “hyopsodontids” at the familial level. Additional justification for this action is presented with the results of the phylogenetic analysis. Apheliscidae Matthew, 1918 has priority over Louisininae Sudre and Russell, 1982 as the name for “hyopsodontids” other than *Hyopsodus*.

Subfamily Apheliscinae Matthew, 1918

Included genera.—*Apheliscus* Cope, 1875, *Phenacodaptes* Jepsen, 1930, *Gingerichia* gen. nov., possibly *Epapheliscus* Van Valen, 1966.

Age and distribution.—Late Paleocene and early Eocene of western North America and possibly late Eocene or early Oligocene of Italy.

Revised diagnosis.—Apheliscines can be distinguished from other apheliscids by the following combination of features: p4 and P4 larger than preceding and succeeding teeth; p4 with large, tall protoconid; p4 paraconid and metaconid small or absent; p4 talonid simple, with basin weak to absent, and with single prominent cusp; lower molar protoconids and metaconids with inflated bases; lower molar buccal cingulids absent or present only in hypoflexids; paracone of P4 inflated, protocone small; P4 metacone absent or very weak; centrocrista of M1–3 interrupted at midlength because premetacrista begins buccal to termination of postparacrista.

Discussion.—The Apheliscinae previously comprised two North American genera, *Phenacodaptes* and *Apheliscus*, and a European genus, *Epapheliscus*. The single species of *Epapheliscus*, *E. italicus*, is known only from its holotype, a maxilla from the late Eocene or early Oligocene of Italy (Dal Piaz 1930). Van Valen (1966) lists the type specimen as MGP 6834, and describes it as a maxilla with P4–M3. MGP 6834 is actually a maxilla with only P3 and is the type of *?Dyspterna helbingi* Dal Piaz, 1930. The maxilla with P4–M3 to which Van Valen is clearly referring is unnumbered and was initially identified as cf. *Dyspterna woodi* (Dal Piaz 1930). This specimen (MGP unnumbered) and not MGP 6834 is actually the type of *E. italicus*. Based on Dal Piaz’s (1930) illustrations, *Epapheliscus italicus* differs from other apheliscines in several respects, including its retention of strong internal conular cristae and its complete lack of a protocone on P4. As we have not seen the original specimen, it would be premature to completely dismiss a relationship to apheliscines. Other taxa, including artiodactyls, amphilemurid erinaceomorphs, and primates, are not dissimilar; a relationship to one of these groups would make considerably more temporal and biogeographic sense.

Phenacodaptes is represented by a single late Tiffanian species, *Phenacodaptes sabulosus* (Jepsen 1930; Rose 1981; Winterfeld 1982). *Apheliscus* includes the Clarkforkian *Apheliscus nitidus* (Simpson 1937b; Rose 1981) and at least three Wasatchian species (Cope 1874; Matthew 1918; McKenna 1960; Delson 1971; Bown 1979; Rose 1981; Gingerich 1994; Penkrot 2002). Rose (1981) discussed nomenclatural problems within the genus. He noted that intermediate forms blur the distinction between *Apheliscus* and *Phenacodaptes*, a possibility also raised by McKenna (1980). Van Valen (1967) described a new apheliscine genus, *Parapheliscus*, and two new species, *P. bjorni* and *P. wapitiensis*, but Delson (1971) demonstrated that the type specimen of *P. bjorni* is referable to *Phenacolemur* and considered *P. wapitiensis* a junior synonym of *Apheliscus nitidus*. Rose (1981) suggested that *A. wapitiensis* may be valid but, in any case, *Parapheliscus* is not. Gingerich (1994) revalidated *A. wapitiensis* as a rare, small species of the genus and established a new species, *A. chydaeus*, for larger early Wasatchian *Apheliscus* that is nevertheless still smaller than both Clarkforkian *A. nitidus* and later Wasatchian *A. insidiosus*.

Genus *Gingerichia* nov.

Apheliscinae, new genus Youzwysyn 1988: 209.

Apheliscinae, new genus Fox 1990: 59.

Hyposodontidae, new genus Krause and Maas 1990: 84.

Type species: Gingerichia geoteretes sp. nov.

Included species: The type, *G. hystrix* sp. nov., and *G.* sp. 1.

Derivation of the name: Named for Professor Philip D. Gingerich of the University of Michigan in recognition of his important contributions to the study of early Cenozoic mammals.

Age and distribution.—Early Tiffanian (Ti1; earliest late Paleocene) of Montana and Alberta.

Diagnosis.—*Gingerichia* has several autoapomorphies that distinguish it from *Phenacodaptes* and *Apheliscus*: p4 protoconid inflated and somewhat recurved posteriorly; p4 talonid small and simple, either unicuspid or with very small second cuspid; p4 buccal enamel ventrally extended beneath talonid; lower molar buccal cingulids completely absent, including hypoflexid; P4 paracone inflated. Additionally, *Gingerichia* lacks the synapomorphies that unite *Phenacodaptes* and *Apheliscus*: postvallid of p4 and prevallid of P4 vertical; p4 talonid unbasined; p4–m3 with salient posterior cingulids; m1–3 paraconids and paracristids weak to absent; m1–2 hypoconulid enlarged relative to hypoconid and entoconid; P4 protocone strongly reduced; upper molars quadrate rather than wider transversely; M1–2 with straight, nonsalient postmetacrista; M1–2 hypocones reduced and shifted buccally; M1–2 postparaconule cristae weak to absent, such that posterior cingulum reaches metastyle.

Gingerichia geoteretes sp. nov.

Figs. 1–3, Tables 1–3.

Hyposodontidae, new genus and species Krause and Maas 1990: 84.

Holotype: UM 83932 (Fig. 1A), left dentary with p4m1–3 and alveoli for p2–3. Collected by E.M. Schloeder.

Type locality: Douglass Quarry in the eastern Crazy Mountains Basin, south-central Montana, USA.

Hypodigm: UM 83933, right dentary with p4m1–3 and alveoli for p2–3; UM 84535, right dentary with p4m1–3; UM 83939, right dentary with m2–3 and alveoli for p2–3m1; UM 83937, right p2 or p3; UM 83934, right p4; UM 83938, left m1; UM 54888 right m2; UM 83935, right m2; UM 83936, right m2; UM 84536, left m2; UM 84539, left M?2; UM 54889 left M1 or M2 (Figs. 1B, 2A, C).

Derivation of the name: Greek *geios* (of the earth) and *teretes* (keeper, watcher) (Brown 1956), in reference to the EARTHWATCH organization, whose volunteers found several specimens of this new species. Gender: masculine.

Referred material.—Glennie Quarry, eastern Crazy Mountains Basin, south-central Montana: UM 54890, left p4 in dentary fragment; UM 54891, right P4; UM 54894, right P4; UM 54893, left P4; UM 54892, right M?1 (Figs. 2B, 3).

Age and distribution.—*Gingerichia geoteretes* is known from Douglass Quarry (the type locality) and from Glennie Quarry, both of which are of early Tiffanian (Ti1) age (Krause and Gingerich 1983; Hartman and Krause 1993).

Diagnosis.—*Gingerichia geoteretes* is distinguishable from *G. hystrix* based on the following characteristics: larger size

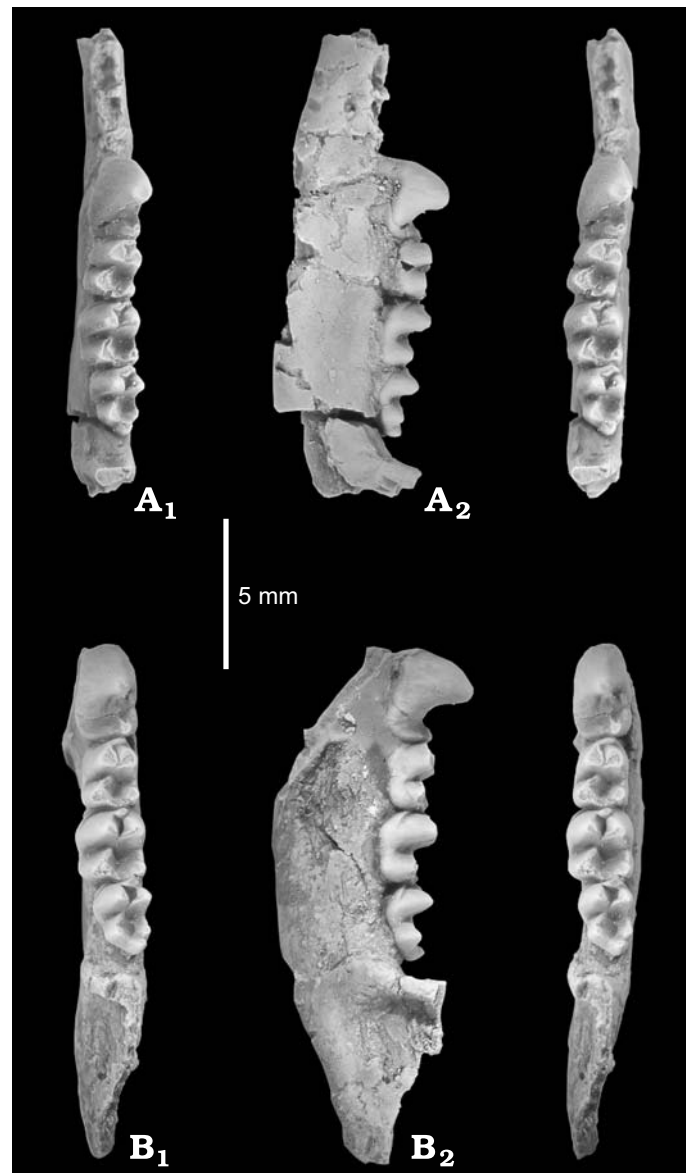


Fig. 1. Dentaries of *Gingerichia geoteretes* gen. et sp. nov. from the early Tiffanian Douglass Quarry, Montana, USA. A. Holotype, left p4–m3, UM 83932 in occlusal (A₁, stereophotograph) and buccal (A₂) views. B. Right p4–m3 (reversed), UM 84535 in occlusal (B₁, stereophotograph) and buccal (B₂) views.

(see diagnosis of *G. hystrix*, Tables 1 and 2); more robust and bunodont cheek teeth; less exodaenodonty in p4–m3; p4 talonid erect, not anteriorly recurved; m1–2 trigonids lower and talonids more elongate; m1–3 paraconids crestiform; M1 more quadrate. See Tables 1 and 2 for measurements.

Description.—The dentary is shallow, approximately 3.4 mm deep below m1 (Fig. 1). The four alveoli anterior to p4 preserved in UM 83933 are small and closely appressed, presumably for two-rooted p2 and p3. Two mental foramina are preserved on UM 83933, one below the anterior part of the posterior alveolus for p3 and the other below the anterior part of the posterior alveolus for p2.

Table 1. Measurements of *Gingerichia* lower dentitions. Abbreviations: L, length; T, type specimen; TAW, talonid width; TRW, trigonid width; W, width. All measurements in millimeters.

Specimen #	p2 or 3 L	p2 or 3 W	p4 L	p4 W	m1 L	m1 TRW	m1 TAW	m2 L	m2 TRW	m2 TAW	m3 L	m3 TRW	m3 TAW
<i>Gingerichia geoteretes</i>													
Douglass Quarry													
UM 83932 (T)			2.95	1.75	2.25	1.60	1.70	2.70	2.00	1.90	2.60	1.60	1.35
UM 54888								2.50	2.15	2.10			
UM 83933			2.80	1.80	2.30	1.70	1.80	2.30	2.05	1.95	2.50	1.70	1.40
UM 83934			2.90	1.70									
UM 83935								2.45	1.95	1.90			
UM 83936								2.40	2.00	2.00			
UM 83937	1.80	1.15											
UM 83938					2.20	1.50	1.60						
UM 83939								2.45	1.95	1.95	2.50	1.70	1.40
UM 84535			3.00	1.85	2.35	1.65	1.70	2.40	2.15	2.10	2.50	1.60	1.40
UM 84536								2.40	1.90	1.95			
Glennie Quarry													
UM 54890			2.80	1.80									
<i>Gingerichia hystrix</i>													
Cochrane 2													
UALVP 43082 (T)			2.40	1.45									
UALVP 25053			2.70	1.40									
UALVP 25057								2.50	2.10	1.95			
UALVP 25061				1.55									
UALVP 25062			2.50	1.50									
UALVP 25065				1.65									
UALVP 25066						1.50							
UALVP 25067												1.40	
UALVP 25068								2.30	1.90	1.80			
UALVP 25071												1.40	
UALVP 40796			2.75	1.55									
UALVP 42406								2.55	2.00	1.90			
UALVP 42544			2.90	1.70									
UALVP 42634					2.05	1.45	1.50						
UALVP 42642					2.20	1.40	1.65						
UALVP 43083												1.50	
UALVP 43086												1.40	
UALVP 43087							1.55						
<i>Gingerichia</i> sp. 1													
Bingo Quarry													
UM 54895			2.30	1.30									

An isolated, two-rooted p2 or p3 (UM 83937) is referred to *G. geoteretes* on the basis of its size and morphological similarity to p4 (Fig. 2C). It is about 60% the length of p4 (Table 1). The trigonid has a single, prominent, bulbous cusp, the protoconid, which has an apical wear facet. There is no vestige of an anterior cingulid, paraconid, or metaconid. A faint ridge extends down the anterolingual face of the protoconid from the cusp tip and bends slightly more lingually at the base, where it becomes more prominent. Poste-

riorly, a ridge extends from the tip of the protoconid, down the postvallid, and slightly lingually to the base of the single, prominent, posterolingual talonid cusp.

The fourth lower premolar is the largest mandibular tooth in length and height; its width is exceeded only by that of m2 (Figs. 1, 2, Table 1). The two roots are widely separated. The trigonid, which is considerably higher than the talonid, is unicuspid with a large, bulbous protoconid located centrally; there is no trace of either a paraconid or metaconid. An ante-

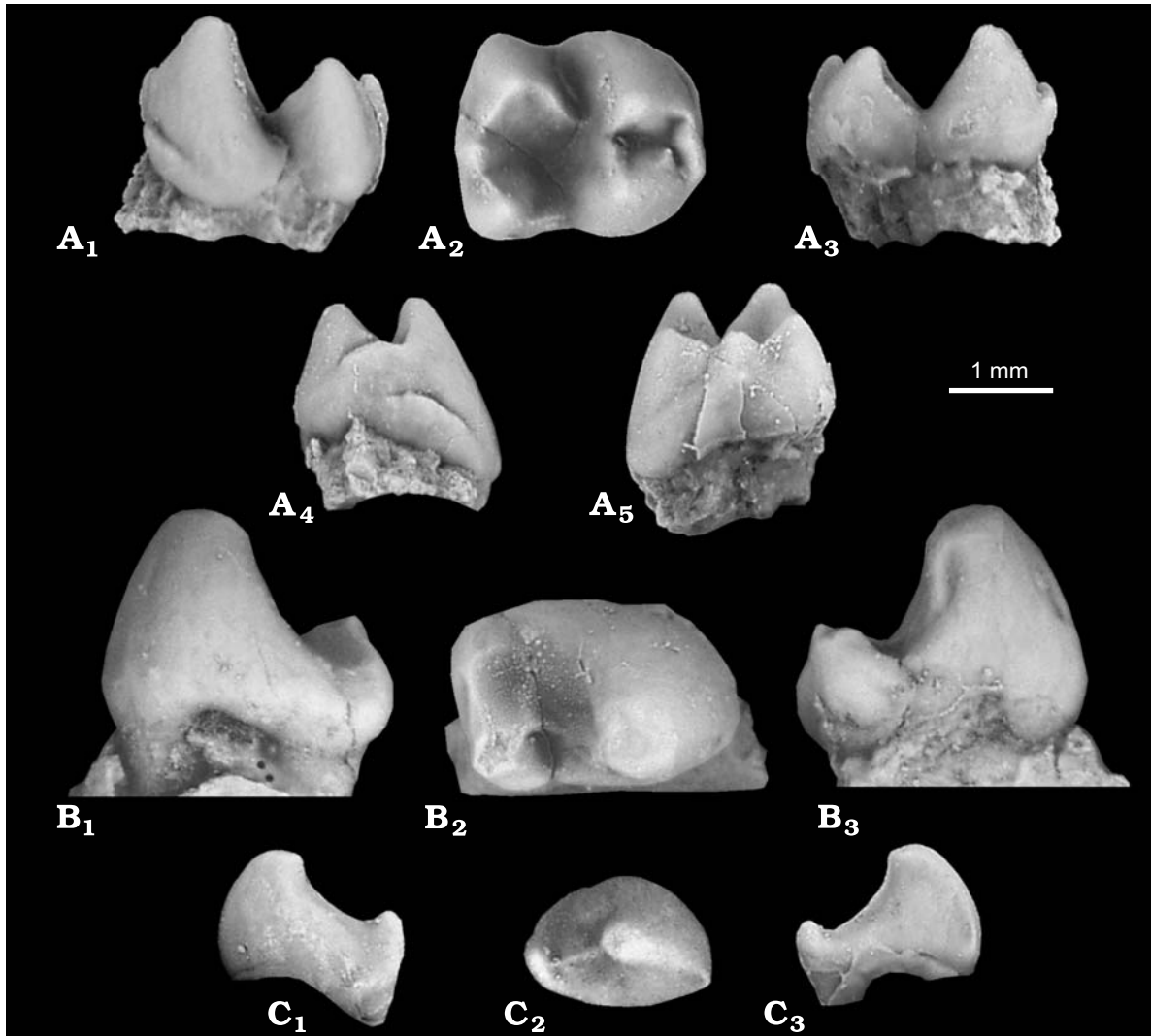


Fig. 2. Lower teeth of *Gingerichia geoteretes* gen. et sp. nov. from the early Tiffanian Douglass (A, C) and Glennie (B) quarries, both Montana, USA. A. Left m2, UM 84536 in buccal (A₁), occlusal (A₂), lingual (A₃), anterior (A₄) and posterior (A₅) views. B. Left p4, UM 54890 in buccal (B₁), occlusal (B₂), and lingual (B₃) views. C. Right p2 or p3 (reversed), UM 83937 in buccal (C₁), occlusal (C₂), and lingual (C₃) views.

rior cingulid is present on p4 of the type specimen, feebly developed on UM 83933, and absent on UM 84534 and UM 84535. In lateral profile, the anterior border of the trigonid is markedly convex and the posterior border is concave. A ridge descends posteriorly from the apex to the base of the protoconid, lingual to the midline. Wear is largely confined to the apex of the protoconid; postvallid wear facets are absent. The talonid is transversely broad. On the type specimen (UM 83932) and UM 83933 there is a single, low, lingual talonid cusp, but on UM 83934 and UM 84535 a second small cusp can be distinguished, just lingual to the main talonid cusp. The cristid obliqua is short and distinct on UM 83932, UM 83933, and UM 83934, but faint on UM 84535. It extends anteriorly from the main talonid cusp and ends buccal to the termination of the ridge that extends posteriorly from the protoconid. On the buccal surface of the tooth, the enamel beneath the talonid of p4 extends further ventrally than the enamel beneath the trigonid.

The molar proportions of *G. geoteretes* are distinctive (Fig. 1). The second lower molar is longer than m1 but slightly shorter than m3, and broader than either m1 or m3 (Table 1). The trigonid and talonid of both m1 and m2 are subequal in width; the m3 trigonid is markedly broader than the talonid (Table 1).

On m1 a distinct, curved paracristid connects the protoconid with a small, terminal paraconid, which lies anterior and slightly buccal to the metaconid. The metaconid is subequal in size to the protoconid and both are much larger than the paraconid. Both metaconid and protoconid have broad, bulbous bases and are closely appressed. Both the anterior and posterior cingulids are poorly developed (particularly so in UM 83933), and there is no vestige of a buccal cingulid. The hypoconulid is the smallest and lowest of the three talonid cusps and is situated approximately midway between, and slightly posterior to, the hypoconid and entoconid. The talonid is deeply basined and is bounded

buccally by a cristid obliqua that meets the trigonid slightly buccal to the midline and to the notch between metaconid and protoconid. The postcristid is continuous between the three major talonid cusps (Fig. 2).

The m2 paracristid turns more sharply at midlength than on m1 and terminates in a small paraconid that is more medial in position than on m1. The paraconid lies slightly lingual to the midline and anterior to the notch between metaconid and protoconid. It is closely appressed to both the metaconid and protoconid; consequently the paracristid is short and the trigonid anteroposteriorly compressed. As in m1 the metaconid and protoconid are subequal in size, broad-based, and closely appressed, there is no buccal cingulid, and the posterior cingulid is indistinct. The anterior cingulid is slightly more pronounced than on m1. The relative size, shape, and position of the three major talonid cusps are virtually identical with those on m1. An entoconulid, absent on the available specimens of m1, is evident on two (UM 83933 and UM 83935) of the eight m2s.

The m3 paracristid, as on m2, is angled but it is more prominent than on m2 and terminates in a larger, more lingually placed paraconid. The protoconid and metaconid are subequal in size but less bulbous and closely appressed than on m1 or m2. The hypoconulid is much more prominent than on the more anterior molars. It is taller than either the hypoconid or entoconid, and more lingual than the m1–2 hypoconulids. An entoconulid is present on two of four specimens. The cristid obliqua curves buccally, in contrast to the straight cristid obliqua on m1 and m2.

The P4 of *Gingerichia* is similar to that of other aphelescids in being dominated by a large, inflated paracone, and a small protocone (roughly one-third to one-half the height of the paracone), also with a bulbous base (Fig. 3). The protocone is positioned slightly anterior to the center of the paracone. A tiny metacone is present, but is essentially fused to the base of the large paracone, and is located along the postparacrista. A small but distinct parastyle is present. The P4 of *Gingerichia* has both an anterior and a posterior cingulum, but these cingula do not meet as the buccal margin of the paracone and the lingual margin of the protocone lack cingula. The posterior cingulum is elevated adjacent to the metacone, where it continues above the level of the rest of the posterior cingulum. Mirroring the posterolingually recurved protoconid of the p4, the P4 paracone is also distinctively recurved posterolingually. Although on a much smaller scale, the parastyle shares this posterolinguall recurvature.

Upper molars of *G. geoteretes* are limited to two fragmentary specimens from Douglass Quarry and a complete but worn molar from Glennie Quarry (Fig. 3). Based on the limited material available, the upper molars of *G. geoteretes* do not appear to differ appreciably in morphology from those of *G. hystrix* (see below). The probable M1 from Glennie Quarry (UM 54892) is somewhat less transverse than a probable M1 of *G. hystrix*, indicating more quadrate upper molars in *G. geoteretes*.

Table 2. Measurements of *Gingerichia* upper dentitions. Abbreviations: L, length; W, width; TRW, trigonid width; TAW, talonid width. All measurements in millimeters.

Specimen #	P4 L	P4 W	M1or2 L	M1or2 W
<i>Gingerichia geoteretes</i>				
Douglass Quarry				
UM 54889			>1.70	>2.80
UM 84539			>2.05	>3.35
Glennie Quarry				
UM 54891	2.65	3.00		
UM 54892			2.20	3.00
UM 54893	2.50	2.80		
UM 54894	2.60	2.70		
<i>Gingerichia hystrix</i>				
Cochrane 2				
UALVP 25050			2.30	3.55
UALVP 25058			2.30	3.55
UALVP 25060	2.45	2.95		
UALVP 25063			2.30	
UALVP 25069	2.15	2.55		
UALVP 42546			2.20	3.10
UALVP 43084				3.30
UALVP 43088			2.30	3.40

Discussion.—Aside from material from the type locality, a small but significant collection of isolated teeth from Glennie Quarry, which lies stratigraphically below Douglass Quarry, is referred to *G. geoteretes*. The Glennie Quarry sample is of importance because it includes well-preserved P4s, which

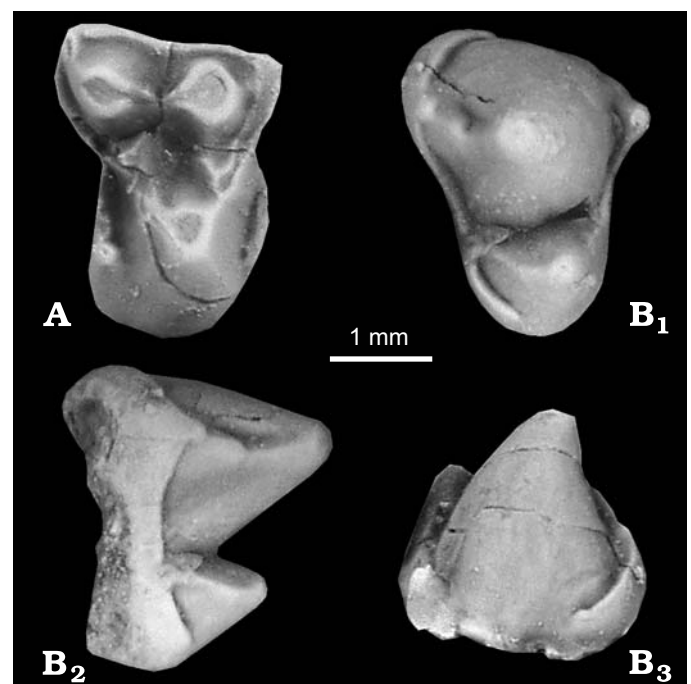


Fig. 3. Upper teeth of *Gingerichia geoteretes* gen. et sp. nov. from the early Tiffanian Glennie Quarry, Montana, USA. A. Right M1?, UM 54892 in occlusal view. B. Right P4, UM 54891 in occlusal (B₁), posterior (B₂), and buccal (B₃) views.

are otherwise represented for the genus by two poorly preserved specimens of *G. hystrix* (see below). Referral of the Glennie Quarry sample to *G. geoteretes* rather than to *G. hystrix* is based on the close match in size and morphology of the single p4 in the Glennie Quarry sample to the type sample from Douglass Quarry.

Gingerichia hystrix sp. nov.

Figs. 4A–E, 5, Tables 1–3.

Apheliscinae, new genus and species Youzwyshyn 1988: 209.

Apheliscinae, new genus and species Fox 1990: 59.

Holotype: UALVP 43082, left p4 (Fig. 4A).

Type locality: Cochrane 2 in the Porcupine Hills Formation, southwestern Alberta.

Typodigm: UALVP 40796, right p4; UALVP 42544, right p4; UALVP 25053, left p4; UALVP 25061, left p4; UALVP 25062, left p4; UALVP 25065, left p4; UALVP 25066, right m1; UALVP 42642, right m1; UALVP 43087, right m1; UALVP 42634, left m1; UALVP 25057, right m2; UALVP 42406, right m2; UALVP 25068, left dentary fragment with m2 and alveoli for p4–m1 and m3; UALVP 25067, right m3; UALVP 43083, right m3; UALVP 25071, left m3; UALVP 43086, left m3; UALVP 25060, left P4; UALVP 25069, right P4; UALVP 42546, right M?1; UALVP 25058, left M?2; UALVP 43088, left M?2; UALVP 25050, right M1 or M2; UALVP 25051, left M1 or M2; UALVP 25052, right M1 or M2; UALVP 25054, left M1 or M2; UALVP 25059, left M1 or M2; UALVP 25063, right M1 or M2; UALVP 43084, right M1 or M2; UALVP 43085, right M1 or M2.

Derivation of the name: *Hystrix*, the Latin name for the Old World porcupine. Named in reference to the Porcupine Hills and Porcupine Hills Formation. Obliquely, also a reference to the sharper cusps relative to those of the type species.

Age and distribution.—*Gingerichia hystrix* is known only from the type locality, Cochrane 2, which is of early Tiffanian (Ti1) age (Youzwyshyn 1988; Fox 1990; Scott et al. 2002).

Diagnosis.—*Gingerichia hystrix* is distinguishable from *G. geoteretes* based on the following characteristics: smaller size (p4 area averages 21% smaller; m1 area averages 18% smaller); more lightly built and less bunodont cheek teeth; p4–m3 more exodaenodont; p4 talonid anteriorly recurved; m1–2 trigonids taller and talonids shorter; retention of conate paraconid on m1–3; M1 more transverse. See Tables 1 and 2 for measurements.

Description.—Lower teeth of *Gingerichia hystrix* specimens from Cochrane 2 tend to be markedly smaller than those from Douglass Quarry, although the small sample of m2s shows no appreciable size difference.

Lower fourth premolars of *G. hystrix* are noticeably more gracile and less bunodont than those of *G. geoteretes* (Fig. 4). In the type p4, a small but distinct paraconid is retained, as is a subtle metaconid “swelling” near the base of the large, recurved protoconid. *Gingerichia hystrix* p4s have a less inflated protoconid base than do those of *G. geoteretes*. The talonid of p4 is less elongate and its cusps taller in *G. hystrix* than in *G. geoteretes*. In addition to being taller, talonid cusps of *G. hystrix* are slightly recurved anteriorly, a feature not found in *G. geoteretes*. Finally, *G. hystrix* p4s show

Table 3. Summary statistics for *Gingerichia geoteretes* and *G. hystrix*. Abbreviations: N, sample size; μ , mean; OR, observed range. All measurements in millimeters.

		<i>G. geoteretes</i>			<i>G. hystrix</i>		
		N	μ	OR	N	μ	OR
P4	L	3	2.58	2.50-2.65	2	2.30	2.15-2.45
	W	3	2.83	2.70-3.00	2	2.75	2.55-2.95
M1 or 2	L	1	–	2.20	5	2.28	2.20-2.30
	W	1	–	3.00	5	3.38	3.10-3.55
p2 or 3	L	1	–	1.80	–	–	–
	W	1	–	1.15	–	–	–
p4	L	5	2.89	2.80-3.00	5	2.65	2.40-2.90
	W	5	1.78	1.70-1.85	7	1.54	1.40-1.70
m1	L	4	2.28	2.20–2.35	2	2.13	2.05-2.20
	TRW	4	1.61	1.50-1.70	3	1.45	1.40-1.50
	TAW	4	1.70	1.60-1.80	3	1.57	1.50-1.65
m2	L	8	2.45	2.30-2.70	3	2.45	2.30-2.55
	TRW	8	2.02	1.90-2.15	3	2.00	1.90-2.10
	TAW	8	1.98	1.90-2.10	3	1.88	1.80-1.95
m3	L	4	2.53	2.50-2.60	–	–	–
	TRW	4	1.65	1.60-1.70	4	1.43	1.40-1.50
	TAW	4	1.39	1.35-1.40	–	–	–

somewhat greater ventral extension (exodaenodonty) of buccal enamel than do p4s of *G. geoteretes*.

Lower molars of *G. hystrix* show similar differences from *G. geoteretes*, with *G. hystrix* having less bunodont molars than the Montana species (compare Figs. 1, 2, and 4). Trigonids of *G. hystrix* molars are relatively higher and more open than those of *G. geoteretes*. In *G. hystrix*, a distinct conate paraconid is retained, whereas in *G. geoteretes* the paraconid is poorly differentiated from the remainder of the paracristid. Finally, molars of *G. hystrix* have relatively shorter talonids than do those of *G. geoteretes*.

P4 of *G. hystrix* is represented by two heavily abraded specimens, which makes comparisons with *G. geoteretes* difficult. From what is preserved, however, they do not appear to differ substantially. In contrast to the sample of *G. geoteretes* from Douglass Quarry, which is dominated by specimens from the lower dentition, that of *G. hystrix* from Cochrane 2 is best represented by M1s and M2s (Fig. 5). As maxillae of *Gingerichia* have yet to be found, it remains impossible to confidently distinguish M1s from M2s. By analogy with *Haplaletes* and *Litomylus*, M1s may differ from M2s in having a hypocone whose base extends further lingually, giving the lingual margin of the crown a straighter margin (compare Fig. 5A₁ with Fig. 5C). On this basis, a few specimens can be tentatively assigned a locus. The upper molars of *Gingerichia* closely resemble those of *Litomylus*, aside from being markedly more transverse. The three primary trigon cusps form an acute triangle, with the paracone and protocone in transverse alignment, and roughly subequal in size. The cusp apices are sharper and less bunodont than in

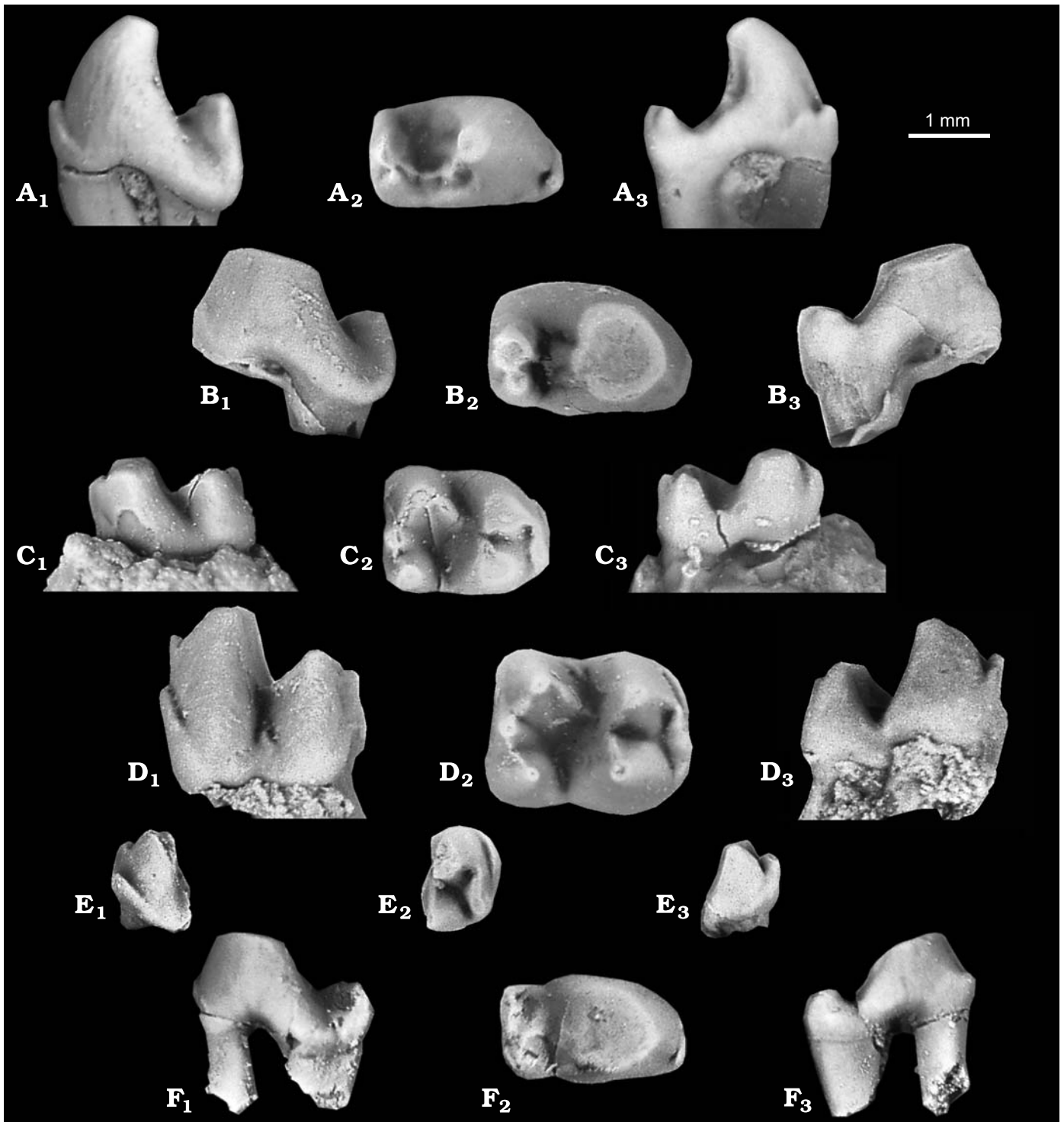


Fig. 4. A–E. Lower teeth of *Gingerichia hystrix* gen. et sp. nov. from the early Tiffanian Cochrane 2 locality, Alberta, Canada. A. Holotype, left p4, UALVP 43082 in buccal (A₁), occlusal (A₂), and lingual (A₃) views. B. Left p4, UALVP 25062 in buccal (B₁), occlusal (B₂), and lingual (B₃) views. C. Left m1, UALVP 42634 in buccal (C₁), occlusal (C₂), and lingual (C₃) views. D. Right m2 (reversed), UALVP 42406 in buccal (D₁), occlusal (D₂), and lingual (D₃) views. E. Left m3 trigonid, UALVP 43086 in buccal (E₁), occlusal (E₂), and lingual (E₃) views. F. *Gingerichia* sp. 1 from the early Tiffanian Bingo Quarry, Montana, USA, right p4 (reversed), UM 54895 in buccal (F₁), occlusal (F₂), and lingual (F₃) views.

Phenacodaptes and *Apheliscus*. The postparacrista and premetacrista are only moderately developed, and they are not continuous (the anterior end of the premetacrista is slightly offset buccally).

There is a strong cingulum wrapping from the antero-lingual margin of the paracone to the posterolingual margin of the metacone. This buccal cingulum is continuous with the paracingulum and preparaconule crista anteriorly and the

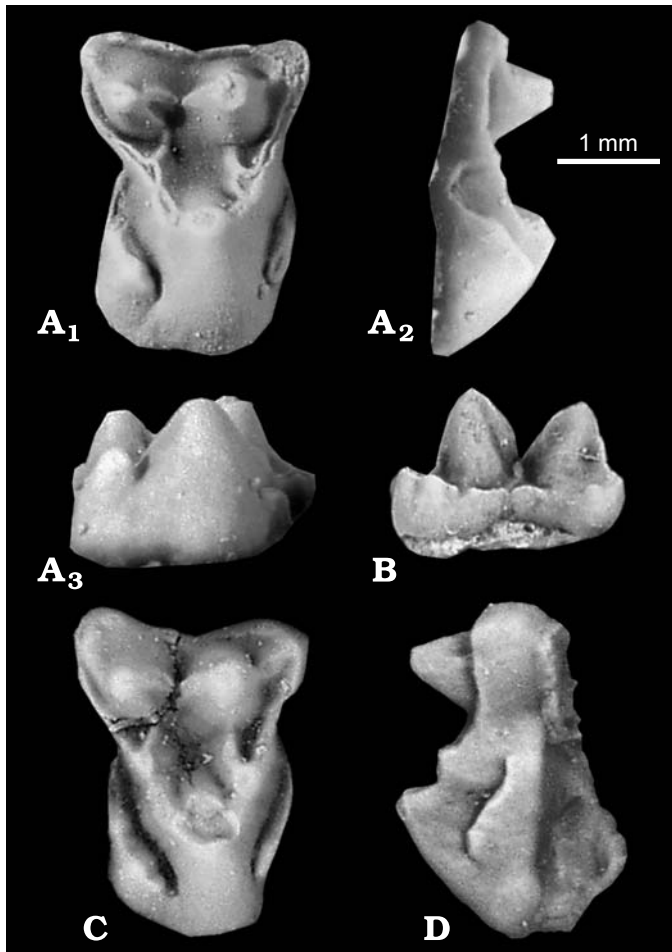


Fig. 5. Upper teeth of *Gingerichia hystrix* gen. et sp. nov. from the early Tiffanian Cochrane 2 locality, Alberta, Canada. **A.** Right M1?, UALVP 42546 in occlusal (A₁), posterior (A₂), and lingual (A₃) views. **B.** Right M1 or M2, UALVP 25063 in buccal view. **C.** Left M2? (reversed), UALVP 43088 in occlusal view. **D.** Right M1 or M2, UALVP 43084 in anterior view.

metacingulum and postmetaconule crista posteriorly. The parastyle is low and more shelflike than connate. The metastyle is somewhat more distinct, and is located at the posterior end of a well-defined postmetacrista. The preparacrista, though present, is relatively more weakly developed. The parastyle and metastyle produce winglike extensions of the buccal cingulum at the anterior and posterior corners of the molars, respectively, resulting in a weak ectoflexus. Both the paraconule and metaconule are present, but the paraconule is more strongly developed and is displaced slightly lingual relative to the metaconule. Additionally, while both internal conular cristae are present, the postparaconule crista is much stronger than the premetaconule crista. Strong pre- and postprotocristae connect the conules to the protocone.

A small anterior cingulum, which extends for the entire breadth of the protocone, ends just anterior to the paraconule and does not contact the buccal cingulum. There is a strong hypocone, which arises out of a moderate posterior cingulum. This posterior cingulum does not contact the buccal cingulum, but rather dives under it at the point where the

postmetaconule crista and the buccal cingulum become continuous.

Discussion.—The distinctiveness of the Cochrane 2 material was first recognized by Youzwshyn (1988) as *Apheliscinae* n. gen. and sp. in an unpublished masters thesis. We maintain that there is sufficient justification for separating the known specimens of *Gingerichia* into two species, centered on the Cochrane 2 and Douglass Quarry populations. In area, *Gingerichia* p4s and m1s from Cochrane 2 are markedly smaller than those from Douglass Quarry (see Table 3 for summary statistics on each species). Particularly in p4, the specimens from Douglass Quarry are noticeably larger than the Cochrane 2 specimens. Additionally, the p4 talonid is relatively more elongate in the Douglass Quarry specimens. In the Cochrane 2 *Gingerichia* specimens, p4 and the lower molars show greater distention of buccal enamel than do the Douglass Quarry specimens, and the p4 talonid cusps are recurved anteriorly. Lower molars from Cochrane 2 have relatively higher and more open trigonids and shorter talonids than do specimens from Douglass Quarry, and retain a connate paraconid (whereas in the Douglass Quarry specimens it is nearly indistinguishable from the paracristid). Finally, the cheek teeth in the Douglass Quarry specimens are more bunodont than in the Cochrane 2 sample.

The size and morphological distinctions between Cochrane 2 and Douglass Quarry specimens of *Gingerichia* are sufficiently great to warrant their separation into two species. Differences between the two samples are consistent with those recently used to distinguish species of other apheliscid genera, particularly species of *Apheliscus* (Gingerich 1983, 1994; Penkrot 2002). In fact, the morphological differences between the Douglass Quarry and Cochrane 2 samples exceed the morphological differences between some apheliscid species (e.g., *Aletodon mellon*–*A. gunnelli*; *Haplomyilus speirianus*–*H. scottianus*; Gingerich 1983, 1994).

Where they differ morphologically, *G. hystrix* is generally less specialized than *G. geoteretes*. In particular, p4s of *G. hystrix* are less simplified and inflated. This suggests that *G. hystrix* may have been ancestral to *G. geoteretes*, which in turn would suggest that Cochrane 2 is somewhat older than Douglass Quarry. This is consistent with Youzwshyn's (1988) assessment that other elements of the fauna are more primitive than those at Douglass Quarry.

Gingerichia sp. 1

Fig. 4F, Table 2.

Referred material.—UM 54895, right p4.

Age and distribution.—*Gingerichia* sp. 1 is known only from Bingo Quarry in the eastern Crazy Mountains Basin, south-central Montana, which is of early Tiffanian (Ti1) age (Hartman and Krause 1993).

Description.—UM 93348 is heavily worn, which limits the amount that can be said about it. The protoconid is large, as in other *Gingerichia*, but probably somewhat less inflated. A very small paraconid connected to a short, weak anterior

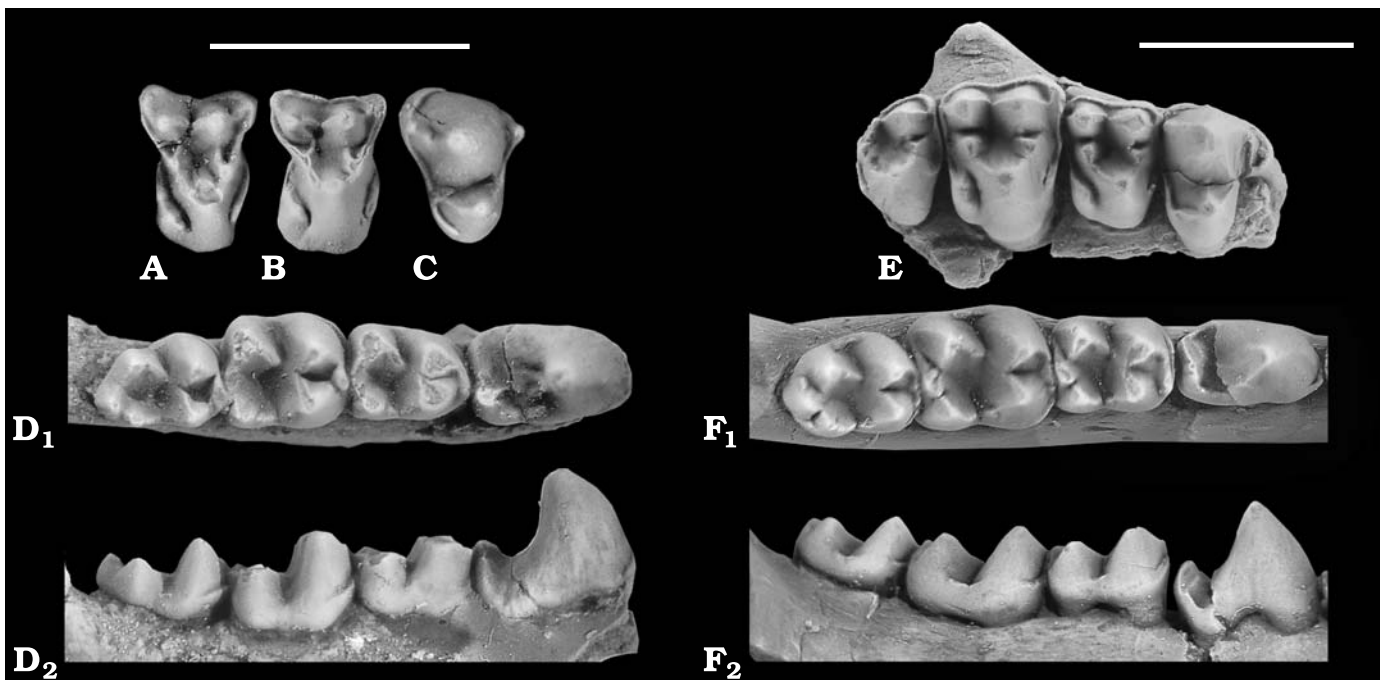


Fig. 6. Comparison of the dentitions of *Gingerichia* spp. from the early Tiffanian of Montana, USA and Alberta Canada (A–D) and *Phenacodectes sabulosus* from the middle Tiffanian of Wyoming (E, F). A–C. Composite upper dentition of *Gingerichia* spp. in occlusal view. A. *G. hystrix*, left M2? (reversed), UALVP 43088. B. *G. hystrix*, right M1?, UALVP 42546. C. *G. geoteretes*, right P4, UM 54891. D. *G. geoteretes*, right dentary with p4–m3, UM 84535 in occlusal (D₁, reversed) and buccal (D₂) views. E. *P. sabulosus*, left maxilla with P4–M3, YPM:PU 17591 in occlusal view (reversed). F. *P. sabulosus*, left dentary with c, p2–m3 (p4–m3 shown), YPM:PU 14398 in occlusal (F₁) and buccal (F₂, reversed) views. Scales bars 5 mm.

cingulid is retained. The degree of wear makes it impossible to determine if a metaconid was present as well. The talonid appears to have been bicuspid, although the buccal cusp has been largely obliterated by wear. Although small, the talonid of UM 93348 is somewhat wider and more basined than in other p4s of *Gingerichia*. As is typical of the genus, the buccal enamel beneath the talonid is distended ventrally. The posterior cingulid is sharper than in other *Gingerichia* p4s, potentially a reflection of the generally less inflated crown.

Discussion.—A probable third species of *Gingerichia* is represented by a single, worn p4 from Bingo Quarry, the earliest Tiffanian locality in the Crazy Mountains Basin. The very small size, weakly inflated p4 trigonid, and less reduced talonid of UM 93348 appear to be primitive features for Apheliscinae and argue against its allocation to either *G. geoteretes* or *G. hystrix*. We consider it inadvisable, however, to name a new species of apheliscine on the basis of a single worn tooth. UM 93348 is nonetheless significant as it provides the most plesiomorphic record of the genus, while demonstrating that the distinctive features of both Apheliscinae and *Gingerichia* were already developed in the earliest Tiffanian.

Bingo Quarry lies stratigraphically below both Douglass and Glennie quarries (Hartman and Krause 1993), both of which have yielded specimens of *G. geoteretes* (see above). *Gingerichia* species 1 appears not only to be primitive relative to *G. geoteretes* from Douglass and Glennie quarries but

also relative to *G. hystrix* from Cochrane 2. This suggests that Cochrane 2 is younger than Bingo Quarry but older than Douglass and Glennie quarries. Discovery of *G. hystrix* in the Crazy Mountains Basin would provide a test of this tentative conclusion.

Discussion

Comparisons of *Gingerichia* with other apheliscines.—Comparisons of *Gingerichia* with other small-bodied Paleogene mammals indicate that its closest affinities are with the Apheliscinae. *Gingerichia* shares the following character states with other apheliscines: enlargement of p4 relative to m1; enlarged, tall protoconid on p4 and paracone on P4; reduction of other cusps on P4 and p4 trigonid; narrow p4 talonid, lacking cristid obliqua, and with single well-developed cusp; presence of well-defined molar anterior cingulid; reduction of molar buccal cingulids; and centrocrista on upper molars interrupted at midpoint. The lower dentition of *Gingerichia* differs from those of *Phenacodectes* and *Apheliscus* in the complete absence of a paraconid and metaconid from p4, in the retention of a distinct, small paraconid on m2 and m3, in the greater relief between the trigonid and talonid, the absence of molar buccal cingulids, and in the more median position of the hypoconulid on m1–2. The upper dentition of *Gingerichia* differs from that of *Phenacodectes* and *Apheliscus* in having a more inflated P4 paracone, more

transverse upper molars, a stronger, more lingually positioned hypocone on M1–2, and in retaining complete external conular cristae (Fig. 6). Of these features, those involving p4 and P4 are most likely derived. The absence of any vestige of the buccal cingulid also appears to be derived for the group. The stronger hypocone of *Gingerichia*, while frequently a derived character among “condylarths,” may be plesiomorphic in this case, as there appears to be a trend toward hypocone reduction going from *Phenacodaptes* to early *Apheliscus* species to later *Apheliscus* (TAP unpublished data). The relatively flat postvallid of *Phenacodaptes* and *Apheliscus* bears a strong posterior facet; in contrast, the homologous facet is poorly developed or lacking in *Gingerichia*. Instead, the apex of the protoconid bears a flat, horizontal wear facet. This difference in wear pattern, along with the trend within *Gingerichia* species toward increased bunodonty, suggests greater specialization for hard-object feeding in *Gingerichia* relative to other apheliscines, as a tendency toward increased shearing predominates in the *Phenacodaptes*–*Apheliscus* lineage. Given the small size of *Gingerichia*, this could denote specialization for predation on either some variety of seed or particularly tough-shelled invertebrates.

Possible affinities of apheliscines.—As discussed in the introduction, apheliscine affinities have been controversial, with postulated relationships to “hyopsodontid” and mioclaenid “condylarths” and pentacodontid pantolestans (Gazin 1959; McKenna 1960; Van Valen 1967, 1978; Rigby 1980; Rose 1981; McKenna and Bell 1997; Archibald 1998). The identification of *Gingerichia* as the likely sister taxon to previously known apheliscines provides an opportunity to revisit the question of apheliscine affinities, as *Gingerichia* retains several plesiomorphic features that are lost or modified in later members of the clade. Morphological similarities between the dentitions of apheliscines and pentacodontids (particularly *Aphronorus* and *Pentacodon*) have been discussed by a number of workers (e.g., Gazin 1959; McKenna 1960; Rigby 1980). As in pentacodontids, the p4 of *Gingerichia* and other apheliscines is enlarged relative to m1. However, p4 of Pentacodontidae and Apheliscinae differ significantly in morphology. The pentacodontid p4 is distinctly molariform, with a small paraconid and a metaconid larger than in any apheliscine. The p4 talonid basin is much broader, with two large talonid cusps and a distinct cristid obliqua. All apheliscines also differ substantially from pentacodontids in molar morphology. Pentacodontids (particularly *Aphronorus* and *Pentacodon*) have much less bunodont molars than do apheliscines, with taller trigonids, more transverse upper molars, and generally better-developed crests. While *Gingerichia* is slightly less bunodont than other apheliscines, it is still much more bunodont than either pentacodontid. All apheliscines differ from *Aphronorus* and *Pentacodon* in having larger m2s than m1s, in lacking prominently thickened anterior cingula on upper molars, and in lacking bladellike lower molar paraconids. *Gingerichia* has a more prominent paraconid than do *Phena-*

codaptes and *Apheliscus*, but it remains much less salient than in either pentacodontid genus.

The discovery of *Gingerichia* provides new evidence that some molar similarities shared by *Aphronorus* and *Pentacodon* and later apheliscines are convergent. While *Apheliscus* resembles *Aphronorus* and *Pentacodon* in having a paracone on its upper molars that is much larger than the metacone, the paracones of *Gingerichia* and *Phenacodaptes* are only slightly larger than the metacones, indicating that the similarity between *Apheliscus* and pentacodontids is convergent. *Apheliscus* and *Phenacodaptes* resemble *Aphronorus* and *Pentacodon* in having weak hypocones on their upper molars. The stronger hypocone on *Gingerichia* upper molars again argues that the morphology of later apheliscines is simply convergent on pentacodontids.

In sum, *Gingerichia* in particular, and apheliscines as a group, share inflation of p4 and little else with the Pentacodontidae. Detailed differences in p4 morphology between *Gingerichia* and pentacodontids, as well as evidence derived from the general configuration and relative size of the molars, seems to preclude a close phylogenetic relationship between apheliscines and known Torrejonian and Tiffanian pentacodontids, thus running counter to the arguments of Gazin (1959) and Rigby (1980).

The bunodont molars of *Gingerichia* and other apheliscines are more consistent with affinities to “hyopsodontid” or mioclaenid “condylarths” than pentacodontids. The simple morphology of apheliscine posterior premolars resembles most mioclaenids and contrasts with the relatively molarized premolars found in most “hyopsodontids” (Simpson 1937a; Cifelli 1983; Archibald 1998). The p4 of *Gingerichia* shows a particular similarity to that of the Puercan mioclaenid *Choeroclaenus*, which also has an inflated trigonid and a unicuspid talonid. Premolar morphology alone provides an insufficient basis for aligning apheliscines with mioclaenids, as some “hyopsodontids” (*Haplaletes pelicatus*, *Louisina*, *Microhyus*) also have simple posterior premolars (Gazin 1956; Russell 1964; Antunes et al. 1987). In fact, molar morphology of *Gingerichia* and other apheliscines argues for a closer relationship to “hyopsodontids”.

As it did with pentacodontids, the retention of a paraconid and a well-developed hypocone in *Gingerichia* helps to clarify the potential affinities of apheliscines to “hyopsodontids” and mioclaenids. The weak hypocone of *Apheliscus* was one of the features cited by McKenna (1960) as favoring a relationship to mioclaenids. In most mioclaenids the hypocone is little more than a thickening of the posterior cingulum, in contrast to the well-developed hypocone found in most “hyopsodontids.” The morphology of *Gingerichia* (and to a lesser extent *Phenacodaptes*) closely resembles the condition in “hyopsodontids” and indicates that the reduced hypocone of *Apheliscus* is convergent on mioclaenids.

The paraconid and paracristid of *Gingerichia* lower molars offer particularly strong evidence that apheliscines have “hyopsodontid,” rather than mioclaenid, affinities. In mioclaenids, the paraconid on m2–3 is tall, lingual, and closely appressed to

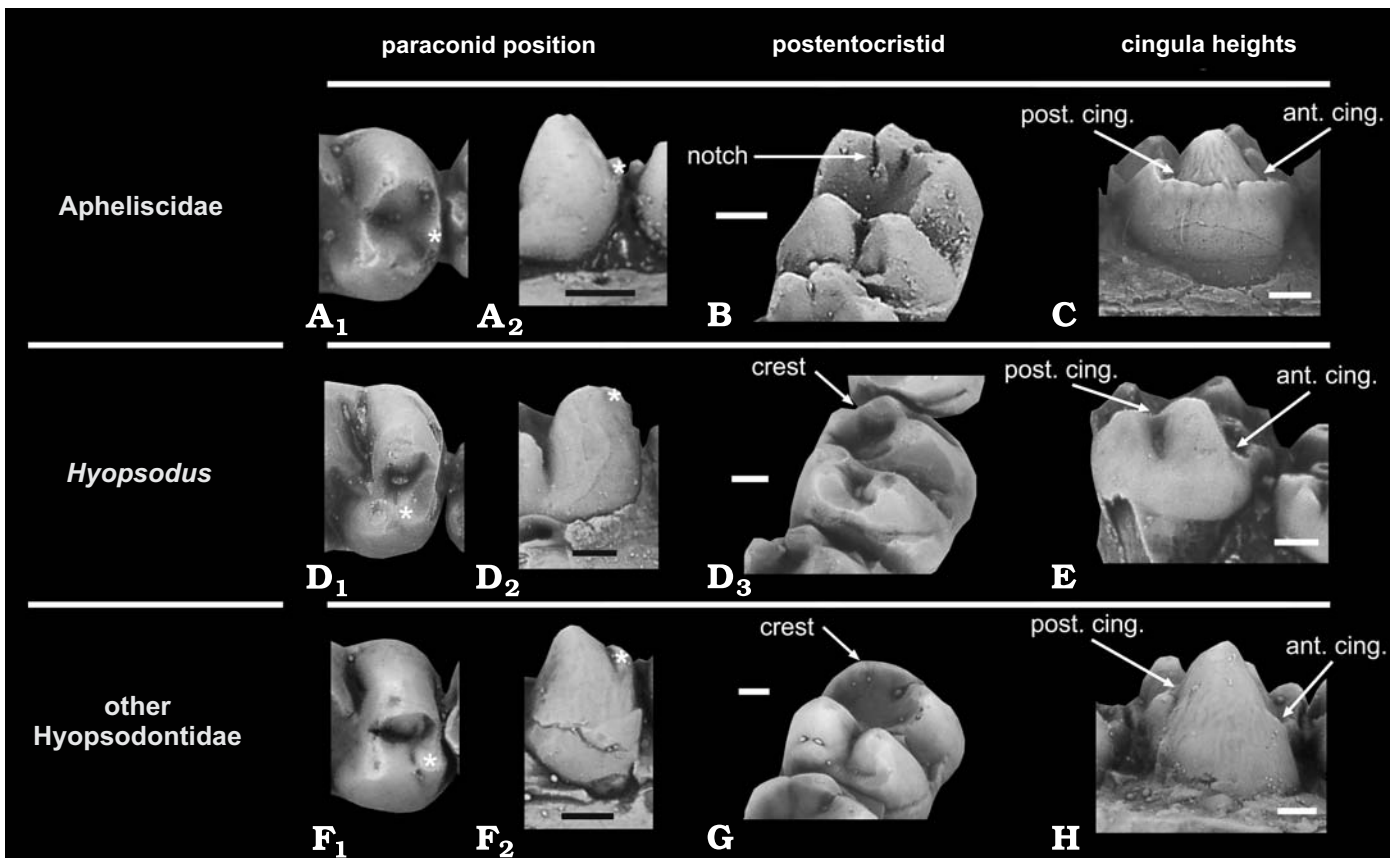


Fig. 7. Comparison of phylogenetically significant dental features in Apheliscidae, *Hyopsodus*, and other Hyopsodontidae to illustrate the differences between apheliscids and hyopsodontids. **A.** *Litomylus dissentaneus*, left m2, USNM 9318 (Torrejonian, Montana, USA). **B.** *Phenacodaptes sabulosus*, left m2, YPM:PU 19504 (Tiffanian, Wyoming, USA). **C.** *Aletodon gunnelli*, right M2, UM 63307 (Clarkforkian, Wyoming, USA). **D.** *Hyopsodus latidens*, left m2, USNM 525587 (Wasatchian, Wyoming, USA). **E.** *Hyopsodus latidens*, right M2, USNM 525388 (Wasatchian, Wyoming, USA). **F.** *Choeroclaenus turgidunculus*, left m2, USNM 15465 (Puercan, New Mexico, USA). **G.** *Promioclauenus lemuroides*, left m2, USNM 407572 (Torrejonian, New Mexico, USA). **H.** *Litaletes disjunctus*, right M2, USNM 9324 (Torrejonian, Montana, USA). The left column compares paraconids (asterisk) on left m2 in occlusal (A₁, D₁, F₁) and lingual (A₂, D₂, F₂) views. The D₃ represents the oblique anterobuccal view of the tooth figured also in D₁ and D₂. The paraconid is low and median in apheliscids but tall, lingual, and basally fused with the metaconid in hyopsodontids. The center column compares postentocristids on left m2 in oblique anterobuccal view. The postentocristid is notched between the hypoconulid and entoconid in apheliscids, while it forms a smooth crest between the hypoconulid and entoconid in hyopsodontids. The right column compares the positions of the anterior cingulum (ant. cing.) and posterior cingulum (post. cing.) on right M2 in lingual view. In apheliscids, both cingula arise from the same level on the base of the protocone, while in hyopsodontids, the posterior cingulum arises higher on the protocone than does the anterior cingulum. Scale bars 1 mm.

the metaconid, to the point that the bases of these cusps are generally fused (Fig. 7). In contrast, most “hyopsodontids” (with the notable exception of *Hyopsodus*) have lower paraconids that are well separated from their respective metaconids and terminate between the protoconid and metaconid rather than reaching the lingual margin of the crown. In all respects, *Gingerichia* matches the “hyopsodontid” condition and contrasts with mioclaenids. Taken in combination with the presence of a strong hypocone and other features that are also retained in *Phenacodaptes* and *Apheliscus*, such as the lack of a crest between the hypoconulid and entoconid on m1–2, the morphology of the paraconid in *Gingerichia* indicates that the relationships of apheliscines lie with “hyopsodontids” and not with mioclaenids.

Phylogenetic analysis.—The comparisons presented above suggest two hypotheses amenable to testing by phylogenetic

analysis. First, *Gingerichia* most strongly resembles the apheliscines *Apheliscus* and *Phenacodaptes* and it may be hypothesized that these taxa share a closer relationship with each other than any does with other small, bunodont Paleocene–Eocene eutherians. Second, the relationships of this group lie with “hyopsodontids” and not with mioclaenids or pentacodontids. For the most part, these hypotheses can be tested by a phylogenetic analysis of Hyopsodontidae *sensu lato*, which we present below. The potential for a relationship between apheliscines and pentacodontids, which may be phylogenetically distant from “condylarths,” cannot be completely addressed in this work, although we do provide a preliminary test.

Methods.—To test these hypotheses, a character–taxon matrix was constructed including 59 characters scored for 24 of the best known representatives of “Hyopsodontidae” and

Mioclaenidae, as traditionally defined, as well as two outgroups, Zhelestidae and the basal “condylarth” *Protungulatum donnae* (Appendices 1–3). To evaluate the possibility of a relationship between apheliscines and pentacodontid “pantolestans,” characters were also scored for the pentacodontid *Aphronorus*. Characters were taken from the cheek dentition and proximal tarsus. Some dental characters are modified from Muizon and Cifelli (2000), Tabuce et al. (2001), and Hooker and Dashzeveg (2003). Additional dental characters were constructed, where necessary, to account for the dental diversity of the ingroup. Tarsal morphology was included in the analysis because recent discoveries indicate considerable morphological diversity in this area (Muizon et al. 1998; Godinot et al. 1996; Penkrot et al. 2003; Zack et al. 2005), although the tarsus is only known in a subset of the ingroup (*Hyopsodus*, *Choeroclaenus*, *Molinodus*, *Paschatherium*, *Haplomylus*, *Apheliscus*). Cranial characters were not considered because the cranium is well known only in *Hyopsodus*. Character states of 16 characters with three or more states form plausibly linear transformation series and were treated as ordered in some analyses.

The composition of one taxon included in the analysis, *Utemylus*, is novel and warrants comment. Gingerich (1983) named *Utemylus latomius* for a maxilla with M1–3 and a referred P4, both from the late Tiffanian (Ti4) of Mason Pocket in the northern San Juan Basin. In the course of making comparisons for this study, we observed that one late Tiffanian taxon known only from lower molars, *Haplaletes serior* Gazin, 1956 from the Bison Basin *Titanoides* locality, shows features that would be expected of the lower dentition of *Utemylus*. Most notably, the lower molars of *H. serior* show strong exodaenodonty and general transverse skewing such that the lingual sides of the crowns are elevated relative to the buccal sides. This matches well with the upper molars of *U. latomius* in which the buccal sides of the crowns are elevated and there is strong distention of enamel beneath the lingual ends of the crowns. Additionally, there is a generally good occlusal fit, particularly with regard to the degree of reduction of m3 and M3. When combined with similarities in size and age, this suggests that *Haplaletes serior* represents the lower dentition of *Utemylus latomius* or a close relative. Accordingly, we remove *H. serior* from *Haplaletes* to *Utemylus* as *Utemylus serior* comb. nov. and use it to code the lower dentition of the genus. The morphologic distance separating *U. latomius* and *U. serior* from the type species of *Haplaletes*, *H. disceptatrix*, justifies generic distinction of *Utemylus* from *Haplaletes*.

All analyses were performed using the parsimony ratchet algorithm of NONA v2.0 (Goloboff 1999) spawned by Winclada (BETA) v0.9.9 (Nixon 1999b). The parsimony ratchet algorithm allows rapid analysis of relatively large data sets while circumventing islands of relatively but not optimally short trees by reweighting a random subset of characters during each run of a heuristic search (Nixon 1999a). To ensure that the shortest trees were recovered, ten repetitions of each analysis were performed. A total of four analy-

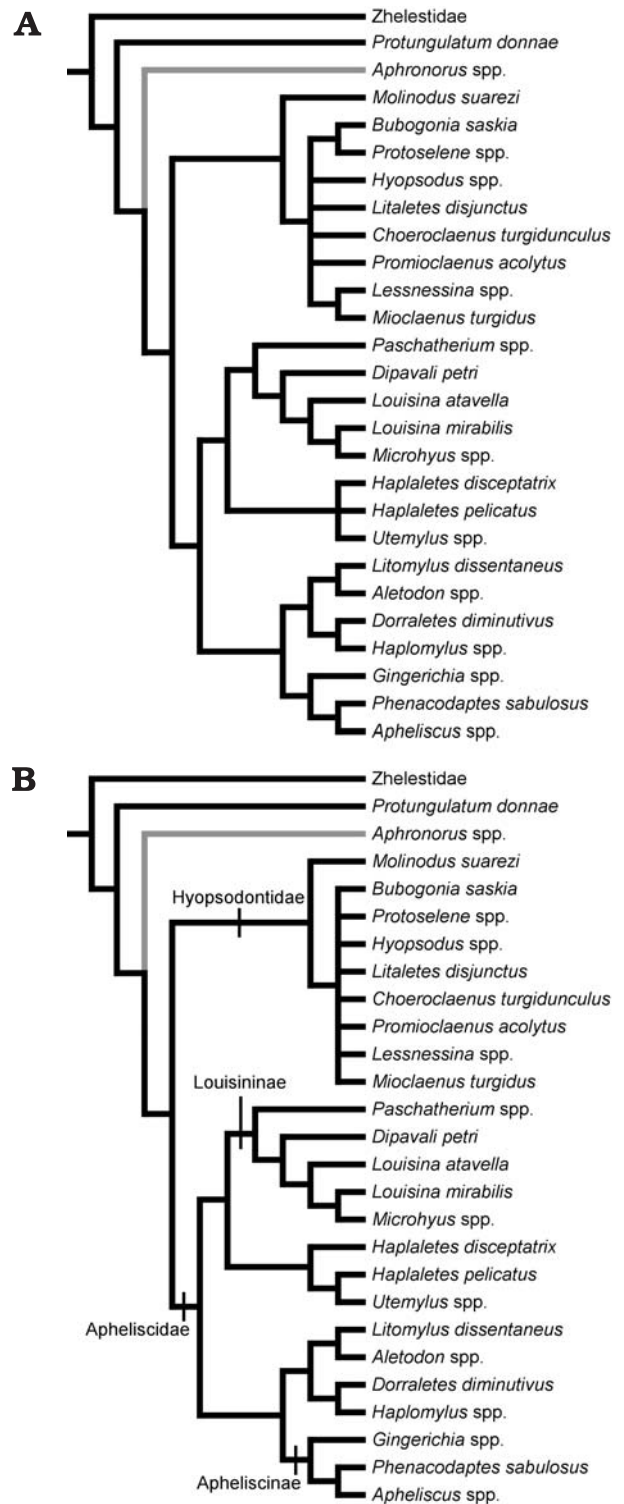


Fig. 8. Phylogenetic relationships of “hyopsodontids,” mioclaenids, and *Aphronorus*. **A**. Results with all characters unordered. **B**. Results with some characters ordered. In **A**, black lines represent the strict consensus of six trees, while in **B**, black lines represent the strict consensus of ten trees. In both trees, the gray line indicates the position of *Aphronorus* when that taxon is included. In both cases, with *Aphronorus* included, the number of most parsimonious trees remains the same, while inclusion of *Aphronorus* does not affect the topology of the remainder of the ingroup. See text for tree statistics. The consensus presented in **B** is our preferred tree. Named nodes correspond to the new classification proposed in this work.

ses were performed. First, the matrix was analysed with all characters unordered and all taxa included. In the second analysis, all characters remained unordered, but *Aphronorus* was excluded. These two taxonomic sets (with or without *Aphronorus*) were then run with the 16 potentially ordered characters treated as ordered in the remaining two analyses. Initial runs with *Aphronorus* included consistently placed the latter taxon between the two intended outgroups, rather than within the ingroup. To force ingroup monophyly, ten dummy characters were added to the matrix. For each of these characters, the two outgroups were scored “0” and all ingroup taxa were scored “1,” such that they are parsimony uninformative with respect to the ingroup. With the addition of these dummy characters, all trees recovered had a monophyletic ingroup. When calculating tree statistics, these characters were deactivated.

Results.—When all characters were treated as unordered and all taxa were included, six trees of length 197 steps (CI:39; RI:59) were recovered, the strict consensus of which is shown in Fig. 8A (black and gray lines). In all trees, Apheliscinae, including *Gingerichia*, is monophyletic and forms part of a larger clade that includes most “hyopsodontids.” This grouping is the sister taxon to a clade containing mioclaenids, *Lessnessina*, and *Hyopsodus*. Resolution within the latter clade is poor. *Aphronorus* is recovered as the sister taxon to the remainder of the ingroup and does not form a clade with Apheliscinae. When *Aphronorus* is excluded from the analysis, six trees are still produced (L:190; CI:40; RI:61), the strict consensus of which (Fig. 8A, black lines only) differs from that of the first analysis only in the absence of *Aphronorus*. With *Aphronorus* included and some characters treated as ordered, a total of ten trees (L:200; CI:38; RI:60) is recovered, the strict consensus of which is shown in Fig. 8B (black and gray lines). The results of this analysis differ from those of the unordered analyses only in having full resolution within the “hyopsodontid” clade and less within the mioclaenid clade. Once again, removal of *Aphronorus* produces ten trees (L:193; CI:39; RI:62) the strict consensus of which differs only in the absence of the latter taxon (Fig. 8B, black lines only). The consensus of the ordered analyses (with or without *Aphronorus*) are our preferred trees, largely because the ordered analyses resolve the trichotomy involving *Haplaletes disceptatrix*, *H. pelicatus*, and *Utemylus* in a manner consistent with our expectations.

Relationship between Pentacodontidae and Apheliscinae.—When *Aphronorus* is included in the analysis, it occupies a basal position as the sister taxon to all remaining members of the ingroup. The failure of the analysis to identify a close relationship between *Aphronorus* and apheliscines supports our contention that the similarities between pentacodontids and apheliscines are the products of convergence. Because a number of taxa such as pantolestids and palaeonodonts that may be phylogenetically intermediate between pentacodontids and “condylarths” were not included in this analysis, this conclusion should be considered preliminary.

Table 4. Revised classification of small-bodied condylarths. *Oxyprimus* and *Oxytomodon* are tentatively placed in Hyopsodontidae rather than Apheliscidae because lower molars of both genera possess hyopsodontid synapomorphies (tall paraconid basally fused to metaconid; crest between hypoconulid and entoconid) and lack apheliscid synapomorphies. The taxonomic association of *Pleuraspidotherium* and *Orthaspidotherium* with *Protoselene* and *Bubogonia* follows Johnston and Fox (1984) and Muizon and Cifelli (2000).

Hyopsodontidae (= Mioclaenidae)

- Lessnessina*
- ?*Oxytomodon*
- ?*Oxyprimus*
- Hyopsodontinae
 - Hyopsodus*
- Mioclaeninae
 - Valenia*
 - Tiznatzinia*
 - Bomburia*
 - Choeroclaenus*
 - Promioclaenus*
 - Ellipsodon*
 - Mioclaenus*
 - Litaletes*
- Kollpaninae
 - Tiucloenus*
 - Pucanodus*
 - Molinodus*
 - Andinodus*
 - Simoclaenus*
 - Escribania*
- Pleuraspidotheriinae
 - Bubogonia*
 - Protoselene*
 - Pleuraspidotherium*
 - Orthaspidotherium*
- Apheliscidae
 - Litomylus*
 - Aletodon*
 - Haplaletes*
 - Utemylus*
 - Dorraletes*
 - Haplomytus*
- Apheliscinae
 - Gingerichia*
 - Phenacodaptes*
 - Apheliscus*
- Louisininae
 - Paschatherium*
 - Dipavali*
 - Louisina*
 - Microhyus*
 - Monshyus*

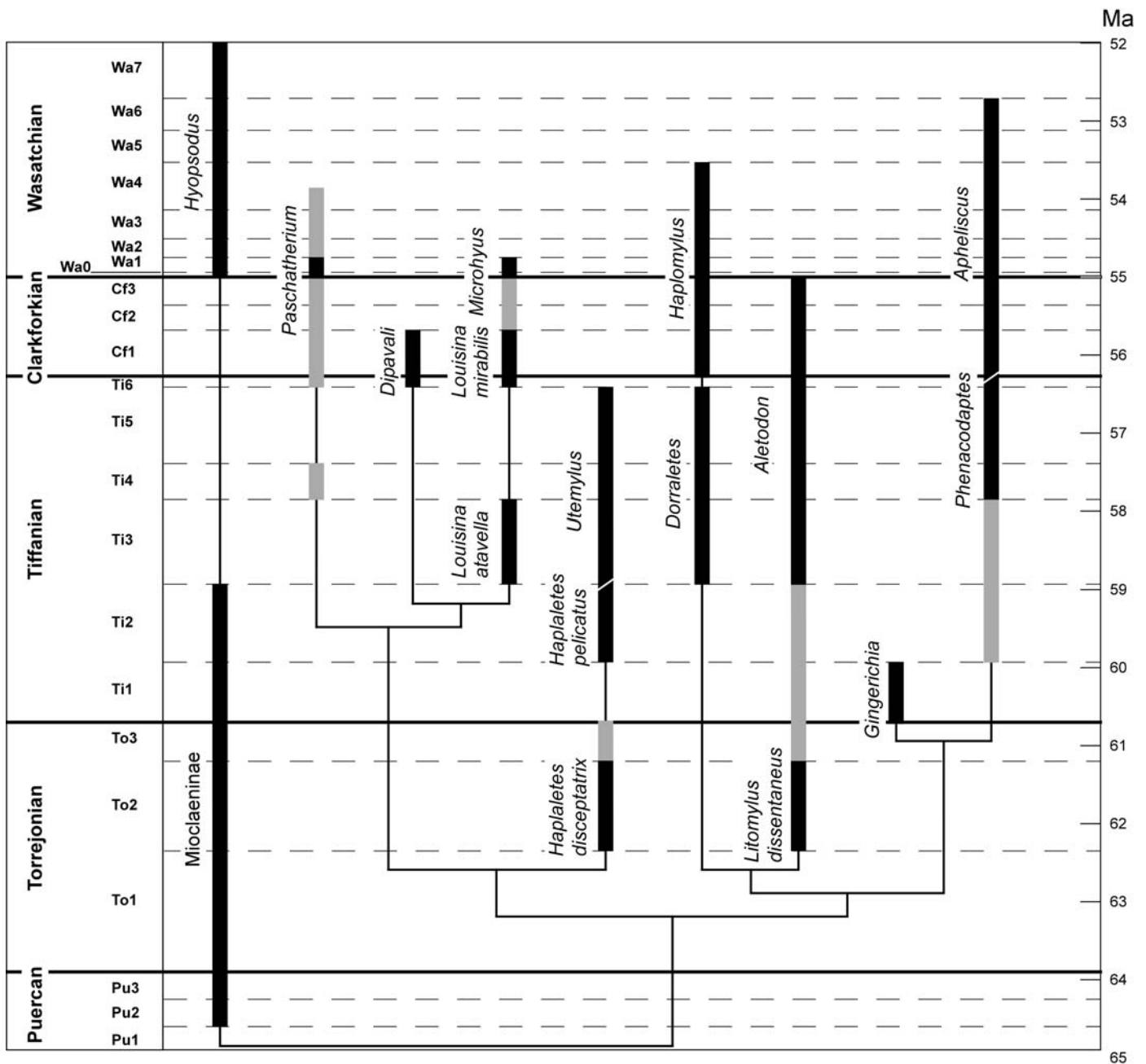


Fig. 9. Phylogeny of Apheliscidae. This figure converts a simplified version of the cladogram in Fig. 8B into a phylogenetic tree, incorporating the authors' subjective opinions of the likelihood that certain taxa may be directly ancestral to taxa included in the analysis. The distinctive but poorly known louisinine *Monshyus* is excluded from this figure, as available material is insufficient to confidently reconstruct its phylogenetic position. Gray bars indicate taxa not included in the analysis that may help complete the record of potential lineages. Biochronology follows Lofgren et al. (2004). Temporal correlations of North American faunal zones follow Williamson (1996), Gengerich (2003), and Lofgren et al. (2004). Correlation of European faunas with North American faunas is largely based on the discussion in Lofgren et al. (2004) and on the correlations of European faunas to the marine record in Smith and Smith (2003).

Status of Hyopsodontidae and Mioclaenidae.—One noteworthy result of the analysis is the position of *Hyopsodus*. Rather than falling with taxa traditionally placed in a restricted “Hyopsodontidae” (excluding Mioclaenidae), *Hyopsodus* is placed with mioclaenids (Fig. 8), in agreement with previous cladistically-based studies of basal ungulate phylogeny (Rigby 1980; Tabuce et al. 2001; Hooker and Dashzeveg 2003). Character

support for this phylogenetic position is strong and includes the presence in *Hyopsodus* of derived features that are otherwise restricted to mioclaenids and the absence of derived features that characterize other “hyopsodontids” (Fig. 7). *Hyopsodus* does share a few derived features with some other “hyopsodontids,” but these are largely traits associated with incipient lophodonty (e.g., strong hypocone; loss of post-

metaconule crista) that have developed independently in numerous other mammalian clades, including probable mioclaenid descendants in the order Litopterna (Muizon and Cifelli 2000).

The association of *Hyopsodus* with mioclaenids makes “Hyopsodontidae,” as used by most recent workers, polyphyletic. Expanding “Hyopsodontidae” to include mioclaenids would conflict with the consensus in the recent literature (McKenna and Bell 1997; Archibald 1998; Muizon and Cifelli 2000) that mioclaenids warrant separation from hyopsodontids at the familial level, a conclusion generally reached through comparisons of mioclaenids with Paleocene “hyopsodontids,” rather than with *Hyopsodus* itself. Additionally, there is evidence that mioclaenids and Paleocene “hyopsodontids” are not sister taxa in the larger context of early ungulates (Rigby 1980; Tabuce et al. 2001; Zack et al. 2005; TAP and SPZ unpublished data). The alternative solution—which is adopted here (Fig. 8B)—is to redefine Hyopsodontidae to include *Hyopsodus*, *Lessnessina*, and mioclaenids while placing other “hyopsodontids” in a separate family, the appropriate name for which is Apheliscidae Matthew, 1918. Accordingly, we subsume Mioclaenidae into Hyopsodontidae and place most “hyopsodontids” in Apheliscidae (Table 4).

Apheliscid interrelationships.—Within Apheliscidae, there is strong support for Apheliscinae in its traditional usage, including *Phenacodaptes* and *Apheliscus*. This is unsurprising, given the highly distinctive dental morphology of these taxa, particularly of p4 and P4. The phylogenetic analysis also confirms the position of *Gingerichia* as the sister taxon to *Phenacodaptes* and *Apheliscus*, justifying the former’s inclusion in Apheliscinae. However, the autoapomorphically inflated premolars of *Gingerichia* indicate that it probably was not ancestral to *Phenacodaptes/Apheliscus*.

Other well-supported clades within Apheliscidae include Louisininae, a *Litomylus/Aletodon* clade, a *Haplaletes/Utemylus* clade, and a *Dorraletes/Haplomytus* clade. In the last three cases, it is possible that the earlier occurring forms (*Litomylus*, *Haplaletes*, and *Dorraletes*) were ancestral to the later forms, but full consideration of these groups must await further study. Tarsal morphology provides the strongest evidence for interrelationships of these five well-supported clades and indicates that Apheliscinae and the *Haplomytus/Dorraletes* clade are more closely related to each other than either is to Louisininae. The position of the remaining groups (for which the tarsus is unknown) on this framework is much more unstable. The most parsimonious placements of the *Litomylus/Aletodon* and *Haplaletes/Utemylus* clades imply considerable homoplasy and alternative positions do not require many additional steps.

The apheliscid part of the tree, which is the most densely sampled, shows a relatively good fit to stratigraphy. When possible ancestor-descendant relationships are considered and poorly known taxa are added to their likely positions on the tree, many lineages have a relatively complete record (Fig. 9). Several of the longest ghost lineages within Aphe-

liscidae involve European Louisininae and probably reflect the generally sparse European record of Paleocene mammals, as compared to the North American record. Among North American taxa, long ghost lineages occur only at the bases of the *Dorraletes/Haplomytus* and the Apheliscinae clades. In both cases, these lengthy ghost lineages are due to *Litomylus dissentaneus*, which forms part of the sister taxon of both clades, and has a considerably earlier first appearance (To2) than either Apheliscinae (Ti1) or the *Dorraletes/Haplomytus* clade (Ti3).

In contrast to the lengthy ghost lineage at its base, the record within Apheliscinae itself appears relatively complete. Although the *Phenacodaptes/Apheliscus* clade does not appear until Ti4, approximately three million years after the first appearance of its sister taxon *Gingerichia*, this gap is largely bridged by fragmentary material from Ti2 (Saddle Locality) and Ti3 (Ledge Locality, Twin Creek Locality) that appears to be related to *Phenacodaptes* (SPZ and TAP personal observations).

Conclusions

Gingerichia represents a distinctive new member of Apheliscinae that extends the record of the group to the beginning of the Tiffanian. The discovery of *Gingerichia* increases the morphological diversity of apheliscines while providing new morphologic evidence that links Apheliscinae with “hyopsodontids” and substantially weakens the evidence for affinities with pentacodontids and mioclaenids. *Gingerichia* itself includes three species from Montana and Alberta, one of which is not named, that together span the earliest portion of the Tiffanian (Ti1). Morphological trends within the genus include increases in size, bunodonty, and the degree to which p4 is inflated. The morphology of p4, which is enlarged, simplified, and inflated, is the most distinctive feature of the genus and should permit easy recognition of *Gingerichia* in faunas beyond those reported here. Phylogenetic analysis of small-bodied “condylarths” supports a link between Apheliscinae and most “hyopsodontids.” *Hyopsodus* itself is allied with mioclaenids, necessitating a shift in the family level nomenclature of small “condylarths.” Hyopsodontidae is revised to essentially include mioclaenids and *Hyopsodus*, while other “hyopsodontids” are placed in a revived Apheliscidae.

Acknowledgments

We are particularly grateful to Richard Fox (UALVP, Canada) and Gordon Youzwyshyn (Grant MacEwan Community College, Edmonton, Alberta, Canada) for permitting us to describe the material from Cochrane 2, and C. Scott (UALVP) for facilitating the loan of specimens. We thank Virginia Heisey (Stony Brook University, New York, USA) for her skillful preparation of the specimens described in this report, Philip Gingerich and Gregg Gunnell (UM, USA), Jin Meng,

Christopher Norris, and Denny Dively (AMNH, USA), and Robert Emry and Robert Purdy (USNM, USA) for the loan of comparative material. We would like to thank J. David Archibald (Department of Biology, San Diego State University, San Diego, California, USA) and Jason A. Lillegraven (Department of Geology and Geophysics, University of Wyoming, Laramie, Wyoming, USA) for helpful reviews that have improved the manuscript. We also wish to thank Kenneth Rose (Johns Hopkins University, Baltimore, Maryland, USA) for access to resources and Doug Boyer (Stony Brook University, Stony Brook, New York, USA) for useful discussions. The field project that resulted in the discovery of specimens of *Gingerichia* has benefited from a variety of funding sources: The University of Michigan Museum of Paleontology (1982), National Geographic Society grant 2655 (1983–1984), EARTHWATCH and the Center for Field Research (1983–1986), National Science Foundation grants DEB 8406707 (1984–1986), DEB 8722539 (1988–1991), and DEB 9211243 (1992–1993), and EAR 0308902 (2003–2005), and the Duke University Research Council (1991, 1993). Specimens from Cochrane 2 were collected by field crew members (primarily Gordon Youzwysyn and Gary Stonley) from the University of Alberta as part of Richard Fox's research program, support for which was provided by NSERC.

References

- Antunes, M.T., Estravis, C., and Russell, D.E. 1987. A new condylarth (Mammalia) from the early Eocene of Silveirinha, Portugal. *Münchner Geowissenschaftliche Abhandlungen A* 10: 219–224.
- Archibald, J.D. 1998. Archaic ungulates ("Condylarthra"). In: C.M. Janis, K.M. Scott, and L.L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*, 292–331. Cambridge University Press, Cambridge.
- Bonaparte, J.F., Van Valen, L., and Kramartz, A. 1993. La fauna local de Punta Peligro, Paleoceno inferior, de la Provincia del Chubut, Patagonia. *Evolutionary Monographs* 14: 1–61.
- Bown, T.M. 1979. Geology and mammalian paleontology of the Sand Creek facies, lower Willwood Formation (lower Eocene), Washakie County, Wyoming. *Memoirs of the Geological Survey of Wyoming* 2: 1–151.
- Bown, T.M., and Schankler, D.M. 1982. A review of the Proteutheria and Insectivora of the Willwood Formation (lower Eocene), Bighorn Basin, Wyoming. *United States Geological Survey Bulletin* 1523: 1–79.
- Brown, R.W. 1956. *Composition of Scientific Words, Revised Edition*. 882 pp. Smithsonian Institution Press, Washington, D.C.
- Cifelli, R.L. 1983. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). *American Museum Novitates* 2772: 1–48.
- Cope, E.D. 1874. Report upon vertebrate fossils discovered in New Mexico, with description of new species. In: *Annual Report, Chief of Engineers, U.S. Army, Appendix FF*, 589–606. Washington, D.C.
- Cope, E.D. 1875. Systematic catalogue of Vertebrata of the Eocene of New Mexico, collected in 1874. *Geographic Explorations and Surveys west of the 100th meridian, G. M. Wheeler, Corps of Engineers, U. S. Army, Washington* 4: 37–282.
- Cope, E.D. 1881. On some Mammalia of the lowest Eocene beds of New Mexico. *Proceedings of the American Philosophical Society* 19: 484–495.
- Dal Piaz, G. 1930. I mammiferi dell'oligocene veneto. Creodonta. *Memorie dell'Istituto geologico della R. Università di Padova* 8: 1–17.
- Delson, E. 1971. Fossil mammals of the early Wasatchian Powder River Local Fauna, Eocene of northeast Wyoming. *Bulletin of the American Museum of Natural History* 146: 305–364.
- Estravis, C. and Russell, D.E. 1992. *Paschatherium marianae*, un nouveau Condylarthra de Silveirinha, Éocène inférieur du Portugal. *Bulletin du Museum National d'Histoire Naturelle, Section C* 14: 185–203.
- Fox, R.C. 1990. The succession of Paleocene mammals in western Canada. In: T.M. Bown and K.D. Rose (eds.), *Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America. Geological Society of America Special Paper* 243: 51–70.
- Gazin, C.L. 1956. Paleocene mammalian faunas of the Bison Basin in south-central Wyoming. *Smithsonian Miscellaneous Collections* 131: 1–57.
- Gazin, C.L. 1959. Early Tertiary *Apheliscus* and *Phenacodaptes* as pantolestid insectivores. *Smithsonian Miscellaneous Collections* 139: 1–7.
- Gazin, C.L. 1968. A study of the Eocene condylarthran mammal *Hyoposodus*. *Smithsonian Miscellaneous Collections* 153: 1–90.
- Gingerich, P.D. 1977. *Aletodon gunnelli*, a new Clarkforkian hyoposodontid (Mammalia, Condylarthra) from the early Eocene of Wyoming. *Contributions from the Museum of Paleontology, The University of Michigan* 24: 237–244.
- Gingerich, P.D. 1983. New Adapisoricidae, Pentacodontidae, and Hyoposodontidae (Mammalia, Insectivora and Condylarthra) from the late Paleocene of Wyoming and Colorado. *Contributions from the Museum of Paleontology, The University of Michigan* 26: 227–255.
- Gingerich, P.D. 1994. New species of *Apheliscus*, *Haplomylus*, and *Hyoposodus* (Mammalia, Condylarthra) from the late Paleocene of southern Montana and early Eocene of northwestern Wyoming. *Contributions from the Museum of Paleontology, The University of Michigan* 29: 119–134.
- Gingerich, P.D. 2003. Mammalian responses to climate change at the Paleocene–Eocene boundary: Polecat Bench record in the northern Bighorn Basin, Wyoming. In: S.L. Wing, P.D. Gingerich, B. Schmitz, and E. Thomas (eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene. Geological Society of America Special Paper* 369: 463–478.
- Godinot, M., Crochet, J.-Y., Hartenberger, J.-L., Lange-Badré, B., Russell, D.E., and Sigé, B. 1987. Nouvelles données sur les mammifères de Palette (Éocène inférieur, Provence). *Münchner Geowissenschaftliche Abhandlungen A* 10: 273–288.
- Godinot, M., Smith, T., and Smith, R. 1996. Mode de vie et affinités de *Paschatherium* (Condylarthra, Hyoposodontidae) d'après ses os du tarse. In: M. Godinot and P.D. Gingerich (eds.), *Paléobiologie et Évolution des Mammifères Paléogènes: Volume Jubilaire en Hommage à Donald E. Russell. Palaeovertebrata* 25: 225–242.
- Goloboff, P.A. 1999. *NONA ver. 2.0*. Published by the author, Tucuman, Argentina.
- Hartman, J.H. and Krause, D.W. 1993. Cretaceous and Paleocene stratigraphy and paleontology of the Shawmut Anticline and the Crazy Mountains Basin, Montana: road log and overview of recent investigations. *Montana Geological Society, South Central Field Conference Guidebook* pp. 71–84.
- Holtzman, R.C. 1978. Late Paleocene mammals of the Tongue River Formation, western North Dakota. *Report of Investigation, North Dakota Geological Survey* 65: 1–88.
- Hooker, J.J. 1979. Two new condylarthra (Mammalia) from the early Eocene of southern England. *Bulletin of the British Museum (Natural History), Geology series* 32: 43–56.
- Hooker, J.J. and Dashzeveg, D. 2003. Evidence for direct mammalian faunal interchange between Europe and Asia near the Paleocene–Eocene boundary. In: S.L. Wing, P.D. Gingerich, B. Schmitz, and E. Thomas (eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene. Geological Society of America Special Paper* 369: 479–500.
- Jepsen, G.L. 1930. Stratigraphy and paleontology of the Paleocene of north-eastern Park County, Wyoming. *Proceedings of the American Philosophical Society* 69: 463–528.
- Johnston, P.A. and Fox, R.C. 1984. Paleocene and Late Cretaceous mammals from Saskatchewan, Canada. *Palaeontographica Abteilung A* 186: 163–222.
- Krause, D.W. and Gingerich, P.D. 1983. Mammalian fauna from Douglass Quarry, earliest Tiffanian (late Paleocene) of the eastern Crazy Mountain Basin, Montana. *Contributions from the Museum of Paleontology, The University of Michigan* 26: 157–196.

- Lofgren, D.L., Lillegraven, J.A., Clemens, W.A., Gingerich, P.D., and Williamson, T. E. 2004. The Puerca Through Clarkforkian Land Mammal Ages. In: M.O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*, 43–105. Columbia University Press, New York.
- Matthew, W.D. 1915. A revision of the lower Eocene Wasatch and Wind River faunas: Order Condylarthra, Family Hyopsodontidae. *Bulletin of the American Museum of Natural History* 34: 311–328.
- Matthew, W.D. 1918. A revision of the lower Eocene Wasatch and Wind River faunas: Insectivora (continued), Glires, Edentata. *Bulletin of the American Museum of Natural History* 38: 565–657.
- McKenna, M.C. 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. *University of California Publications in Geological Sciences* 37: 1–130.
- McKenna, M.C. 1980. Late Cretaceous and Early Tertiary vertebrate paleontological reconnaissance, Togwotee Pass area, northwestern Wyoming. In: L.L. Jacobs (ed.), *Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert*, 321–343. Museum of Northern Arizona Press, Flagstaff, Arizona.
- McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.
- Muizon, C. de. 1992. La fauna de mamíferos de Tiupampa (Paleocene inferior, Formación Santa Lucía), Bolivia. *Fósiles y Facies de Bolivia* 12: 575–624.
- Muizon, C. de and Marshall, L.G. 1987a. Le plus ancien condylarthre (Mammalia) sud-américain (Crétacé supérieur, Bolivie). *Comptes Rendus de l'Académie des Sciences, Serie II* 304: 771–774.
- Muizon, C. de and Marshall, L.G. 1987b. Deux nouveaux condylarthres (Mammalia) du Maastrichtien de Tiupampa (Bolivie). *Comptes Rendus de l'Académie des Sciences, Serie II* 304: 947–950.
- Muizon, C. de and Marshall, L.G. 1991. Nouveaux Condylarthres du Paléocène inférieur de Tiupampa (Bolivie). *Bulletin du Museum National d'Histoire Naturelle, Section C* 13: 201–227.
- Muizon, C. de, Cifelli, R.L., and Bergqvist, L.P. 1998. Eutherian tarsals from the early Paleocene of Bolivia. *Journal of Vertebrate Paleontology* 18: 655–663.
- Muizon, C. de and Cifelli, R.L. 2000. The “condylarths” (archaic Ungulata, Mammalia) from the early Paleocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. *Geodiversitas* 22: 47–150.
- Nessov, L.A., Archibald, J.D., and Kielan-Jaworowska, Z. 1998. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. In: K.C. Beard and M.R. Dawson (eds.), *Dawn of the Age of Mammals in Asia*. *Bulletin of Carnegie Museum of Natural History* 34: 40–88.
- Nixon, K.C. 1999a. *Winclada (BETA) ver. 0.9.9*. Published by the author, Ithaca, New York.
- Nixon, K.C. 1999b. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.
- Novacek, M.J. 1985. The Spedectinae, a new subfamily of hedgehog-like insectivores. *American Museum Novitates* 2822: 1–24.
- Novacek, M.J., Bown, T.M., and Schankler, D.M. 1985. On the classification of the early Tertiary Erinaceomorpha (Insectivora: Mammalia). *American Museum Novitates* 2813: 1–22.
- Penkrot, T.A. 2002. Species composition of *Apheliscus* from the Bighorn Basin, Wyoming, with evidence of anagenetic evolution. *Journal of Vertebrate Paleontology* 22: 96A.
- Penkrot, T.A., Zack, S.P., Rose, K.D., and Bloch, J.I. 2003. Postcrania of early Eocene *Apheliscus* and *Haplomyilus* (Mammalia: “Condylarthra”). *Journal of Vertebrate Paleontology* 23: 86A.
- Rigby, J.K. 1980. Swain Quarry of the Fort Union Formation, middle Paleocene (Torrejonian), Carbon County, Wyoming: geologic setting and mammalian fauna. *Evolutionary Monographs* 3: 1–179.
- Rose, K.D. 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene–Eocene boundary. *University of Michigan Papers on Paleontology* 26: 1–197.
- Russell, D.E. 1964. Les mammifères paléocènes d'Europe. *Memoires du Museum National d'Histoire Naturelle* 13: 1–324.
- Scott, C.S., Fox, R.C., and Youzwshyn, G.P. 2002. New earliest Tiffanian (late Paleocene) mammals from Cochrane 2, southwestern Alberta, Canada. *Acta Palaeontologica Polonica* 47: 691–704.
- Simpson, G.G. 1935. New Paleocene mammals from the Fort Union of Montana. *Proceedings of the United States National Museum* 83: 221–244.
- Simpson, G.G. 1937a. The Fort Union of the Crazy Mountain field, Montana, and its mammalian faunas. *Bulletin of the United States National Museum* 169: 1–287.
- Simpson, G.G. 1937b. Notes on the Clark Fork, upper Paleocene, fauna. *American Museum Novitates* 954: 1–24.
- Smith, T. and Smith, R. 2003. Terrestrial mammals as biostratigraphic indicators in upper Paleocene–lower Eocene marine deposits of the southern North Sea Basin. In: S.L. Wing, P.D. Gingerich, B. Schmitz, and E. Thomas (eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene*. *Geological Society of America Special Paper* 369: 513–520.
- Sudre, J. and Russell, D.E. 1982. Les mammifères Montiens de Hainin (Paléocène moyen de Belgique). Part II: Les Condylarthres. *Palaeo-vertebrata* 12: 173–184.
- Tabuce, R., Coiffait, B., Coiffait, P.-E., Mahboubi, M., and Jaeger, J.-J. 2001. A new genus of Macroscelidea (Mammalia) from the Eocene of Algeria: a possible origin for elephant-shrews. *Journal of Vertebrate Paleontology* 21: 535–546.
- Van Valen, L. 1966. Deltatheridia, a new order of mammals. *Bulletin of the American Museum of Natural History* 132: 1–126.
- Van Valen, L. 1967. New Paleocene insectivores and insectivore classification. *Bulletin of the American Museum of Natural History* 135: 217–284.
- Van Valen, L. 1978. The beginning of the Age of Mammals. *Evolutionary Theory* 4: 45–80.
- Williamson, T.E. 1996. The beginning of the Age of Mammals in the San Juan Basin, New Mexico: biostratigraphy and evolution of Paleocene mammals of the Nacimiento Formation. *Bulletin of the New Mexico Museum of Natural History and Science* 8: 1–141.
- Winterfeld, G.F. 1982. Mammalian paleontology of the Fort Union Formation (Paleocene), eastern Rock Springs Uplift, Sweetwater County, Wyoming. *Contributions to Geology, University of Wyoming* 21: 73–112.
- Youzwshyn, G.P. 1988. *Paleocene Mammals from near Cochrane, Alberta*. 484 pp. Unpublished M.Sc. thesis, University of Alberta, Edmonton.
- Zack, S.P., Penkrot, T.A., Bloch, J.I., and Rose, K.D. 2005. Affinities of “hyopsodontids” to elephant shrews and a Holarctic origin of Afrotheria. *Nature* 434: 497–501.

Appendix 1

Material examined.

Zhelestidae (composite of *Aspanlestes aptap*, *Parazhelestes robustus*, *P. minor*, *Eoungulatum kudukensis*, and *Sorlestes budan*): Nessov et al. 1998

Protungulatum donnae: AMNH 96357, uncataloged tarsals; SMM 62-2028 (type)

Bubogonia saskia: UA 15105 (type), 15108; Johnston and Fox 1984

Protoselene spp.

P. griphus: USNM 15773, 15789 (type), 16182, 16203

P. opisthacus: AMNH 3275 (type); UNM B-1301, B-1375; USNM 15404, 88341, 409144-6

Hyopsodus spp.

H. latidens: USNM 488320, 493898, 521641, 521652, 521661, 525388, 525587, 525589

H. loomisi: UCMP 44781 (type) and uncataloged USNM specimens

H. paulus: Gazin 1968; Godinot et al. 1996

H. sp.: USNM 493782, 495492, 521781; USGS 4725; YPM uncataloged skeleton

Litalesites disjunctus: AMNH 35885; USNM 9281, 9324, 9338, 9582, 9666

Lessnessina spp.

L. packmani: Hooker 1979; Hooker and Dashzeveg 2003

L. praecipuus: Godinot et al. 1987; Hooker and Dashzeveg 2003

L. khushuensis: Hooker and Dashzeveg 2003

Promioclænus acolytus: AMNH 35278, 35778; USNM 9280, 9567, 407566; YPM:PU 17468

Choeroclaenus turgidunculus: AMNH 3291 (type), 16402, 16404; USNM 15465, 404933, 404938, 404940

Mioclænus turgidus: BUNM B-1100A, B-871, NP-141; USNM 155330

Molinodus suarezi: Muizon 1992; Muizon et al. 1998; Muizon and Cifelli 2000

Paschatherium spp.

P. dolloi: IRScNB Lt.M. 22; IRScNB Ct.M. 1258; MNHN D 94; MNHN DO 2, 002; Godinot et al. 1996

P. marianae: Estravís and Russell 1992

Dipavali petri: MNHN Cr-261, Cr-930, Cr-1210, Cr-1835; Russell 1964

Louisina atavella: WB 1, 4, 8, 15; Wa-356, 412

Louisina mirabilis: MNHN-Cr 1264; MNHN Braillon Collection, uncataloged left maxilla with M1-3; Russell 1964.

Microhyus spp.

M. musculus: IRScNB Ht.M. 115

M. reisi: Antunes et al. 1987

Litomylus dissentaneus: AMNH 35922, 35924, 35927, 35928, 35933, 35938; USNM 9557, 9318; YPM:PU 16849

Aletodon spp.

A. gunnelli: UM 63307, 65059, 66301 (type)

A. quadravus: UM 82024 (type); YPM:PU 1963, 21449; Holtzman 1978; Gingerich 1983

A. mellon: USNM 10267; Gingerich 1983

Gingerichia geoteretes and *G. hystrix*: see types, typodigms, and referred materials

Phenacodaptes sabulosus: YPM:PU 13302 (type), 13321, 13962, 13977, 14372, 14398, 14409, 17587, 17591, 17595, 17957, 19504

Apheliscus spp.

A. chydæus: UM 66875 (type); USNM 525597

A. insidiosus: AMNH 15696; USGS 12608; USNM 28328, 494986, 495543, 509579, 510873, 521789, 521790, 521791

A. nitidus: AMNH 15849 (type); UM 69941

A. sp.: USNM 493819, 494896

Haplaletes disceptatrix: USNM 9410, 9555, 9600; YPM:PU 14829, 17547, 19835

Dorraletes diminutivus: UM 27231 (type); Holtzman 1978; Gingerich 1983

Haplomyilus spp.

H. palustris: AMNH 22172; Gingerich 1994

H. simpsoni: UM 65249 (type)

H. speirianus: USNM 488319, 493901, 493936, 512563, 513632, 513655, 521645, 525596

H. sp.: USNM 525612, 525613

Haplaletes pelicatus: USNM 21008 (type), 21009

Utemylus spp.

U. latomius: YPM:PU 14583 (type); Gingerich 1983

U. serior: UW 1078 (type)

U. sp.: YPM uncataloged specimens

Aphronorus spp.

A. fraudator: YPM:PU 14764, 17426, 17494

A. orieli: KU 9538; MCZ uncataloged specimens; UM 81833

Appendix 2

State names and symbols.

1. p4 subequal to m1 or somewhat smaller (0) or markedly larger than m1 (1).
2. p4 paraconid better developed than metaconid (0), as developed as metaconid (1), or weaker than metaconid (2). Ordered.
3. p4 trigonid anteroposteriorly short and high crowned (0) or elongate and low crowned (1).
4. p4 protoconid uninflated or weakly inflated (0), moderately inflated (1), or strongly inflated (2). Ordered.
5. p4 talonid anteroposteriorly elongate (0) or abbreviated anteroposteriorly (1).
6. p4 cristid obliqua contacts back of trigonid at level of notch between protoconid and metaconid (0), more buccally beneath posterior protoconid crest (1), or cristid obliqua absent (2).
7. p4 talonid basined (0) or unbasined (1).
8. Distention of enamel on buccal side of lower molars absent (0), weak (1), or strong (2). Ordered.
9. Lower molar trigonids much higher than talonids (0), somewhat higher than talonids (1), or trigonids and talonids subequal in height (2). Ordered.
10. m1-3 buccal cingulid absent or weak and restricted to hypoflexid (0) or strong and complete at least around the trigonid (1).
11. m1-2 talonids broader than trigonids (0), trigonids and talonids

- subequal in width (1), or trigonids broader than talonids (2). Ordered.
12. m1–3 paraconids tall relative to protoconids and metaconids (0) or low (1).
 13. m2–3 paraconid distinctly separated from metaconid (0) or partially to completely fused to metaconid at base (1).
 14. Paraconid on m1–3 positioned at lingual margin of crown (0) or between protoconid and metaconid (1).
 15. Molar paracristid present and well developed (0) or weak to absent (1).
 16. m1–3 metaconid inflated, size subequal to protoconid (0) or uninflated and smaller than protoconid (1).
 17. m2 cristid obliqua orientation nearly parallel to anteroposterior axis of crown (0) or oriented around 45 degrees to long axis of crown (1).
 18. m1–3 hypoconid much larger than other talonid cusps (0) or reduced in size, smaller than entoconid (1).
 19. Hypoconulid on m1–2 on lingual side of talonid, twinned with entoconid (0), in a median position, separate from hypoconid and entoconid (1), or shifted buccally and twinned with hypoconid (2). Ordered.
 20. Hypoconulid on m1–2 much smaller than entoconid and hypoconid (0), slightly smaller than entoconid and hypoconid (1), or larger than entoconid, slightly smaller than hypoconid (2). Ordered.
 21. Notch in postentocristid between hypoconulid and entoconid on m1–2 present (0) or absent (1).
 22. m1–2 entoconulid absent or very weakly developed (0) or well-developed (1).
 23. m1–2 entocristid present and ascends posterior slope of metaconid to close talonid (0), present and wraps around, but does not ascend the base of the metaconid (1), or present and terminates at the base of the entoconid (2), or extremely faint to absent (3).
 24. m2 entoconid taller than hypoconid (0), subequal in height to hypoconid (1), or lower than hypoconid (2). Ordered.
 25. m3 trigonid width subequal to or slightly wider than m2 trigonid width (0), somewhat narrower than m2 trigonid width (1), or much narrower than m2 trigonid width (2). Ordered.
 26. m3 talonid narrower than m3 trigonid (0) or subequal to trigonid width (1).
 27. m3 talonid elongate (0) or anteroposteriorly compressed (1).
 28. P4 parastyle present and relatively well-developed (0) or weak to absent (1).
 29. P4 metacone absent (0), weakly developed (1), or well developed and well separated from paracone (2). Ordered.
 30. P4 protocone much smaller than paracone (0) or slightly smaller than to subequal to paracone (1).
 31. P4 preprotocrista complete between protocone and parastyle, interrupts anterior cingulum (0) or incomplete such that the anterior cingulum continues to parastyle uninterrupted (1).
 32. P4 postprotocrista complete between protocone and metastyle, interrupts posterior cingulum (0) or incomplete such that the posterior cingulum continues to metastyle uninterrupted (1).
 33. P4 hypocone absent (0) or present (1).
 34. M1–2 paracone subequal in size to metacone (0) or larger than metacone (1).
 35. M1–2 mesostyle absent (0) or present (1).
 36. Ends of postparacrista and premetacrista on M1–2 aligned (0) or anterior end of premetacrista terminates buccal to posterior end of postparacrista (1).
 37. M1–2 preparaconule crista complete from paraconule to parastyle, anterior cingulum terminates against preparaconule crista (0) or preparaconule crista incomplete, anterior cingulum continues to parastyle (1).
 38. M1–2 postmetaconule crista complete from metaconule to metastyle, posterior cingulum terminates against postmetaconule crista (0) or postmetaconule crista incomplete, posterior cingulum continues to metastyle (1).
 39. M1–2 metaconule equidistant between buccal and lingual cusps (0) or shifted linguallly, nearly in line with protocone and hypocone (1).
 40. M1–2 protocone greatly enlarged relative to paracone and metacone (0), larger, but not considerably larger, than paracone and metacone (1), or subequal to or smaller than paracone and metacone (2). Ordered.
 41. M1–2 postprotocrista present (0) or absent (1).
 42. M1–2 postprotocingulum absent (0) or present (1).
 43. M1–2 hypocone small to absent (0), well developed but smaller than protocone (1), or subequal in size to protocone (2). Ordered.
 44. M1–2 pericone absent (0) or present (1).
 45. M1–2 posterior cingulum arises from same level on protocone as anterior cingulum (0) or arises higher on protocone than anterior cingulum (1).
 46. Calcaneal tuber short relative to body of calcaneum (0) or relatively elongate (1).
 47. Fibular facet on calcaneum absent (0), present and relatively flat (1), or present and strongly curved to parallel the curvature of the astragalar trochlea (2). Ordered.
 48. Long axis of ectal facet on calcaneum subparallel to long axis of calcaneum (0), approximately 45 degrees to long axis of calcaneum (1), or nearly perpendicular to long axis of calcaneum (2). Ordered.
 49. Calcaneal ectal facet nearly flat, with a large radius of curvature (0), more strongly curved, with a smaller radius of curvature (1), or sharply divided into a medially facing posterior surface and an anteriorly facing anterior surface (2). Ordered.
 50. Peroneal tubercle anteroposteriorly short (0) or elongate (1).
 51. Medial trochlear ridge of astragalus absent such that medial portion of trochlea faces dorsomedially (0) or present such that medial portion faces medially (1).
 52. Trochlear groove on astragalus shallow (0) or deep (1).
 53. Radius of curvature of lateral trochlear ridge of astragalus greater than that of medial ridge (0) or subequal to radius of medial ridge (1).
 54. Astragalar foramen present (0) or absent (1).
 55. Trochlear articular surface only extends onto posterior surface of astragalus medially (0) or articular surface extends onto posterior surface across width of trochlea (1).
 56. Cotylar fossa on astragalus weak or absent (0), prominent and primarily dorsally oriented (1), or prominent and medially oriented (2). Ordered.
 57. Lateral process on astragalar body formed by lateral projection of ectal facet absent (0) or present (1).
 58. Posteromedial projection of astragalar body absent (0) or present (1).
 59. Long axis of navicular facet of astragalus oriented transversely (0) or more parasagittally (1).

